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Climate and Productivity Affect Total Mercury Concentration and Bioaccumulation Rate of Fish along a Spatial Gradient of Subarctic Lakes

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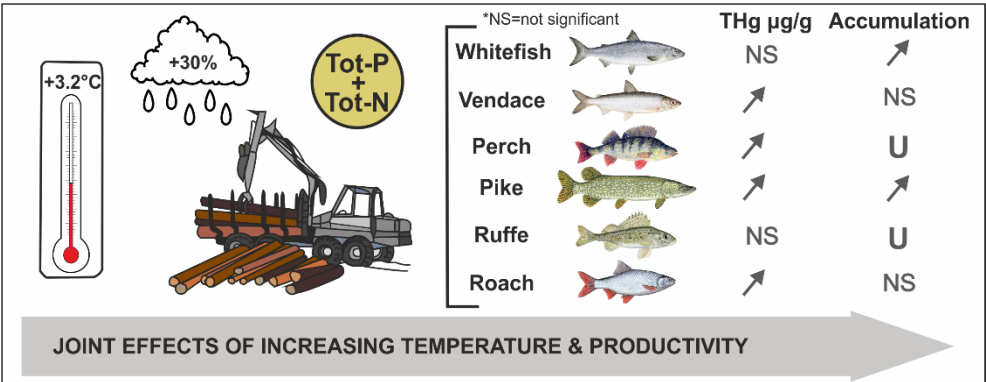
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GRAPHICAL ABSTRACT



HIGHLIGHTS

- Climate and productivity effects on fish mercury (THg) in 18 Subarctic lakes were studied.
- THg concentration and bioaccumulation rates of 6 fish species muscle were examined.
- Temperature and productivity were correlated with THg concentration in 4 species.
- Higher climate-productivity was linked to faster THg bioaccumulation in 2 species.
- Joint environmental stressors should be considered in future THg studies on fish.

21

22 ABSTRACT

23 Climate change is resulting in increased temperatures and precipitation in Subarctic regions of
24 Europe. These changes are extending tree lines to higher altitudes and latitudes, and enhancing tree
25 growth enabling intensification of forestry into previously inhospitable Subarctic regions. The
26 combined effects of climate change and land-use intensification extend the warm, open-water
27 season in Subarctic lakes and increase lake productivity and may also increase leaching and
28 methylation activity of mercury within the lakes. To assess the joint effects of climate and
29 productivity on total mercury (THg) bioaccumulation in fish, we conducted a space-for-time
30 substitution study in 18 tributary lakes of a Subarctic watercourse forming a gradient from cold
31 pristine oligotrophic lakes in the northern headwaters to warmer and increasingly human-altered
32 mesotrophic and eutrophic systems in the southern lower reaches.

33 Increasing temperature, precipitation, and lake productivity were predicted to elevate length- and
34 age-adjusted THg concentrations, as well as THg bioaccumulation rate (the rate of THg
35 bioaccumulation relative to length or age) in muscle tissue of European whitefish (*Coregonus*
36 *lavaretus*), vendace (*Coregonus albula*), perch (*Perca fluviatilis*), pike (*Esox lucius*), roach (*Rutilus*
37 *rutilus*) and ruffe (*Gymnocephalus cernua*).

38 A significant positive relationship was observed between age-adjusted THg concentration and lake
39 climate-productivity in vendace ($r^2=0.50$), perch ($r^2=0.51$), pike ($r^2=0.55$) and roach ($r^2=0.61$). Higher
40 climate-productivity values of the lakes also had a positive linear (pike; $r^2=0.40$) and whitefish
41 ; $r^2=0.72$) or u-shaped (perch; $r^2=0.64$ and ruffe; $r^2=0.50$) relationship with THg bioaccumulation rate.

42 Our findings of increased adjusted THg concentrations in planktivores and piscivores reveal adverse
43 effects of warming climate and increasing productivity on these Subarctic fishes, whereas less
44 distinct trends in THg bioaccumulation rate suggest more complex underlying processes. Joint

45 environmental stressors such as climate and productivity should be considered in ongoing and
46 future monitoring of mercury concentrations.

47

48 KEYWORDS: Climate change; Heavy metal; Intensive forestry; Land use; Temperature

49

50 1. INTRODUCTION

51 Recent climate change has greatly impacted Arctic regions, resulting in temperature and
52 precipitation increases above global average (IPCC, 2015). Furthermore, increased global interests
53 in the Arctic and Subarctic regions are intensifying the resource use in terrestrial and aquatic
54 ecosystems (Huntington et al., 2007; Wrona et al., 2013; Gordon et al., 2018). Enhanced vegetation
55 growth and tree-line extension in the Subarctic, due to climate change, are enabling and intensifying
56 forestry practices associated with peatland ditching and site-preparation practices that expose the
57 mineral soil and increase nutrient and organic carbon run-off (Serreze et al., 2000; Bates et al., 2008;
58 Nieminen et al., 2015). Nutrient and heavy metal loadings are often connected to DOC
59 concentrations, as DOC acts as a carrier of them from catchments to aquatic ecosystem (Porvari and
60 Verta, 2003; de Wit et al., 2014). In freshwater ecosystems, these environmental changes result in
61 an extended open-water season, increased load and concentrations of nutrients and DOC leading
62 to elevated productivity (Karlsson et al., 2009; Sarkkola et al., 2009; Nieminen et al., 2015).

63 Mercury (Hg) is a toxic heavy metal, the methylated form (MeHg) of which bioaccumulates in
64 body tissues of fishes (Morel et al., 1998; Sonesten, 2003a; Trudel and Rasmussen, 2006) and
65 biomagnifies to higher trophic levels in food webs (Jernelöv and Lann, 1971; Morel et al., 1998;
66 Lavoie et al., 2013). Hg originates from natural and anthropogenic sources, but the relative
67 proportion of anthropogenically derived Hg has increased since the Industrial Revolution (Pacyna et
68 al., 2010; UNEP, 2013). In relatively pristine Subarctic regions, Hg primarily enters aquatic

69 ecosystems through atmospheric deposition of inorganic Hg (Schroeder and Munthe, 1998; AMAP,
70 2011; Stern et al., 2012).

71 Methylation of inorganic Hg to MeHg can occur in lake sediment, water column, and in
72 catchment soils, principally by sulphur-oxidizing bacteria (Morel et al., 1998). In Subarctic lakes, the
73 production of MeHg predominantly occurs in the anoxic hypolimnion and lake sediment (Eckley and
74 Hintelmann, 2006), whilst demethylation dominates in the oxygenated photic zone (Morel et al.,
75 1998; Chen et al., 2003). The influence of climate change on methylation-demethylation processes
76 and Hg concentrations in the water and aquatic biota is highly complex and likely system dependent.
77 Mercury methylation rate is positively related to temperature (Bodaly et al., 1993), whereas
78 negative or no connection has been found between demethylation and temperature (Bodaly et al.,
79 1993; Canário et al., 2007). Yang et al. (2016) observed higher MeHg production in warm (+8 °C)
80 versus cold (-2 °C) soils, suggesting an enhanced production of MeHg in the warming Arctic soils. A
81 positive relationship between temperature in lake epilimnion and total mercury (THg) levels in fish
82 was also observed in the Canadian Subarctic (Evans et al., 2005a, b), possibly due to temperature-
83 induced higher net methylation rate and Hg inputs from watersheds.

84 Climate change is resulting in increased leaching of nutrients and DOC in the Subarctic, and this
85 may also be expected to increase the availability of Hg in the water column and aquatic food webs,
86 as DOC is a carrier of Hg (Grigal, 2002; Rydberg et al., 2010). Elevated DOC load is also causing
87 browning and lower light penetration in the water column, which expands the anoxic zone suitable
88 for methylation (Lehnher, 2014; Klapstein et al., 2018). Decomposition of organic matter further
89 stimulates the activity of microbial methylation (Bravo et al., 2017), but DOC also binds Hg, reducing
90 its bioavailability for methylation (Ullrich et al., 2001). The origin of the organic matter has influence.
91 For example, lakes with high levels of algal-derived organic matter exhibit increased bacterial
92 activity and methylation rate. In addition, terrigenous organic matter has been connected to

ultimately higher MeHg concentrations (Bravo et al., 2017). Thus, modification of terrestrial soil, due to intensive forestry, can elevate the availability of MeHg to aquatic systems and wildlife (Morel et al., 1998; Lehnherr, 2014).

Studies assessing how lake productivity influences mercury concentrations and bioaccumulation rates of fishes have, to date, proved inconclusive. In a worldwide study, total phosphorus level was found to have a negative connection to MeHg biomagnification, possible through biomass dilution of THg in primary producers as well as elevated growth rate of organisms at higher trophic levels (Lavoie et al., 2013). A multi-lake study from northeastern North America showed that relatively low productivity in lakes was connected to higher Hg bioaccumulation in food webs (Chen et al., 2005). However, a positive connection between phosphorus level and biomagnification of THg in food webs was found in a Canadian lake (Kidd et al., 2012), and fish communities especially in lakes with forested watersheds were shown to have high concentrations of Hg (Sonesten, 2003b; Chen et al., 2005).

The highest THg concentrations in aquatic biota are generally found in top predators with long lifespans (Cabana and Rasmussen, 1994). Mercury in the water column is integrated into pelagic primary producers by active transport and passive diffusion (Pickhardt and Fisher, 2007), whereas organisms at higher trophic levels predominantly gather Hg from their diet (Hall et al., 1997). The proportion of MeHg of the THg in tissues increases with trophic level, and typically makes up over 90 % of the THg in fish muscle (Watras et al., 1998; Madenjian et al., 2016). Several traits including foraging guilds, thermal guilds, and life-history can all influence the THg concentrations in fish muscle (Trudel and Rasmussen, 2006; Karimi et al., 2016; Thomas et al., 2016). Fish species foraging on pelagic prey typically have higher THg concentrations than benthic feeding fishes, due to higher MeHg concentrations often found in zooplankton than littoral benthic prey (Power et al., 2002; Karimi et al., 2016; Thomas et al., 2016). Moreover, increasing growth rate reduces THg

117 concentrations in fish through growth dilution, while starvation has the opposite effect (Simoneau
118 et al., 2005; Keva et al., 2017).

119 The Subarctic offers a unique region to evaluate the joint effects of climatic and land-use
120 variables on THg concentrations and bioaccumulation rate in fish. Subarctic watercourses represent
121 a gradient ranging from pristine cold and oligotrophic lakes to increasingly human-modified and
122 warmer more productive lakes. This gradient from north to south encompasses the distribution
123 limits of several fish species, as fish communities are dominated by salmonids to percids to cyprinids
124 along increasing air temperature (Hayden et al., 2017). Climate related changes in consumer
125 community structure and functional community structure may also have a significant bearing on the
126 Hg dynamics in Subarctic lakes. Climate change and associated increase in lake productivity are
127 modifying the fish communities in Subarctic lakes as warm-water adapted species are expanding
128 their ranges northwards (Rolls et al., 2017). The presence of novel fish species assemblages modifies
129 consumer community structure, selective foraging, resource competition, and the number of
130 trophic linkages in food webs, all of which can affect Hg burden to piscivores (Thomas et al., 2016).
131 As such, Subarctic environmental gradients represent an opportunity to predict future trends of fish
132 communities and create a realistic natural setting to assess climate and productivity effects on THg
133 in fish at a landscape level (Hayden et al., 2017).

134 We conducted a space-for-time study on a Fennoscandian Subarctic watercourse gradient from
135 north to south to determine how THg concentrations and bioaccumulation rates of six Subarctic fish
136 species are influenced by lake temperature and productivity. The selected fish species are abundant
137 throughout the study area, but differ in their thermal and foraging guilds (Magnuson et al., 1979;
138 Hayden et al., 2013; Thomas et al., 2016). Hg in three generalist species that forage across both
139 pelagic and littoral habitats were assessed: the cold-water adapted European whitefish (*Coregonus*
140 *lavaretus*) that dominate oligotrophic lakes; the cool-water species Eurasian perch (*Perca fluviatilis*)

141 that dominates mesotrophic lakes, and the warm-water species roach (*Rutilus rutilus*) found in
142 eutrophic lakes (Hayden et al., 2017). Perch undergo ontogenetic dietary shifts from zooplankton to
143 benthic macroinvertebrates, and finally to fish prey, whereas whitefish and roach feed almost
144 exclusively on invertebrate prey (Hayden et al., 2014a). In addition, two specialist taxa were studied:
145 vendace (*Coregonus albula*), a cold-water pelagic zooplanktivore, and ruffe (*Gymnocephalus*
146 *cernua*), a cool-water specialist benthivore (Hayden et al., 2013; Thomas et al., 2016). Pike (*Esox*
147 *lucius*), a cool-water obligate piscivore, were also sampled. This species is primarily associated with
148 littoral habitat and feeds on a wide range of prey fish species (Kahilainen and Lehtonen, 2003). All
149 study species forage visually, but percids and cyprinids are more adapted to feeding under increased
150 turbidity than cold-water salmonids (Rolls et al., 2017). Ruffe, perch, and roach are expanding their
151 ranges towards higher latitudes and altitudes in this area (Hayden et al., 2013, 2014a).

152 In the current study, we assessed how climate and lake productivity, lake morphometry and
153 catchment properties influence length- and age-adjusted THg concentrations, and the
154 bioaccumulation rate of THg in whitefish, vendace, perch, pike, roach, and ruffe. Using a space-for-
155 time substitution approach, we tested whether THg concentrations in fish were related to lake
156 temperature-productivity along a Subarctic watercourse with climatic and land-use gradients from
157 north to south (Hypothesis 1). We hypothesized that THg bioaccumulation rates relative to fish
158 length and age (the slope of regression between THg and length or age) would increase along the
159 gradient from north to south (Hypothesis 2), since increase in temperature and productivity of lakes
160 cause shifts in community structure, elevating the amount of pelagic derived energy (Hayden et al.,
161 2017; Leppänen et al., 2017).

162

163 2. MATERIAL AND METHODS

164 2.1. The study sites

165 Eighteen tributary headwater lakes located in the Subarctic Tornio-Muonionjoki watercourse
166 were sampled in northern Fennoscandia (Fig. 1). The lakes are distributed along a climate and
167 productivity gradient from northern to southern Lapland where the open water season air
168 temperature, precipitation, and total phosphorus increased by 3.2 °C (ranging from 8.4 to 11.6 °C),
169 30 % (ranging from 197 to 257 mm), and total 45 µg/L (ranging from 3 to 48 µg/L), respectively (Table
170 1). Conservative climate change models for this region predict increases in temperature and
171 productivity matching the temperature, precipitation, and productivity measured ranges here by
172 the end of this century (IPCC, 2015). Land-use related variables, such as total length of artificial
173 ditches and tree volume in the catchment increased along the same gradient, indicating
174 intensification of land use.

175 Lake characteristics ranged from clear oligotrophic (<15 µg/L total phosphorus) lakes (1–7, 9) in
176 the north to increasingly mesotrophic (15–29 µg/L total phosphorus, lakes 8, 10–13) and eutrophic
177 lakes (>29 µg/L total phosphorus, lakes 14–18) towards the south (Fig. 1, Table 1). The highest
178 latitude lakes (1–7, 9) are surrounded by mountain birch forest, with low human population density
179 and land use consisting mainly of reindeer herding. Theoretical compensation depth, the depth at
180 which 1 % of surface light intensity was detectable, decreases towards the south. The mesotrophic
181 and slightly more colored lake (8) is located below the northern distribution limit of Scots pine (*Pinus*
182 *sylvestris*) with increasing human population density. The lower latitude mesotrophic lakes (10–13)
183 are located below the northern distribution limit of Norway spruce (*Picea abies*) with higher human
184 population density and forestry as well as nature tourism. The eutrophic lakes (14–18) are
185 characterized by the highest human population density in the catchment among the study lakes, as
186 well as intensive forestry, with associated site-preparation and ditching practices, as the principal
187 forms of land use, enhancing nutrient loading to the lakes, and thus increasing the water color
188 (Jussila et al., 2014).

190 *2.2. Environmental variables*

191 The climate and lake environmental variables were primarily obtained from long-term archives.
192 Geographic location and altitude of each lake were obtained from the National Land Survey of
193 Finland. Average air temperature (°C) and precipitation (mm) during the open water season
194 (June–September) were obtained for each lake from long-term data (1981–2010; Finnish
195 Meteorological Institute, Klein Tank et al., 2002) from six weather stations located through the study
196 area (Fig. 1, Table 1). Total phosphorus and nitrogen data were obtained during the fish sampling or
197 regional monitoring programs of the same year (Lapland Centre for Economic Development,
198 Transport and Environment). The lake morphometric variables included lake area (km²), maximum
199 depth (m), mean depth (m) and lake volume (m³) that were obtained from Hertta-database (Finnish
200 Environment Institute) or derived from data of bathymetric maps created by using an echosounder-
201 chartplotter device (LCX-112C GPS-chartplotter: Lowrance, Tulsa, Oklahoma, U.S.A.). Visible light
202 intensity (400–700 nm) was measured in the water column using a LI-COR LI-250A light meter (LI-
203 COR Biosciences, Lincoln, NE, U.S.A.). This data was used to calculate the compensation depth that
204 defined the habitat border between the littoral and pelagic zones. The catchment variables were
205 entirely derived from data archives, where the land-use variables were derived from CORINE Land-
206 Cover data implemented in VALUE-tool (Finnish Environmental Institute). These data were used to
207 calculate catchment area (km²) and relative proportions (%) of different land-use practices (urban,
208 agriculture, forest, sparse vegetation, wetland and water) in catchment and transformed to area
209 coverages e.g. forest (ha). Tree volume data for the forested area was obtained from the open
210 access data bank (The Natural Resources Institute Finland). The total length of artificial ditches (km)
211 in the catchment of each lake was analyzed from open map data (National Land Survey of Finland).

212 Tree volume (m³/ha) and ditch length (km/km²) variables were calculated for forested and wetland
213 catchments. Analyses were conducted using ESRI ArcMap 10.3.1 software.

214

215 *2.3. Fish species and field sampling*

216 We sampled six fish species across the 18 study lakes: whitefish, vendace, perch, pike, roach,
217 and ruffe. Whitefish and pike inhabited almost all the study lakes, whereas perch, roach, and ruffe
218 were absent from the northernmost lakes (Table 2). Vendace and roach were abundant in the lower
219 latitudes. Fish were caught over five consecutive days between late-August and September in
220 2009–2013, to control for potential seasonal THg variation in muscle tissue (Kahilainen et al., 2016;
221 Keva et al., 2017). The target sample size was 30 individuals for each species in each lake, if possible.
222 The fish were caught by gillnet series with eight nets (size: 30 x 1.8 m, knot-to-knot mesh size: 12,
223 15, 20, 25, 30, 35, 45 and 60 mm), as well as one Nordic multi-mesh gillnet (size 30 x 1.5 m, mesh
224 sizes 5–55 mm) with 12 equidistant panels of 2.5 m. Pike samples were supplemented with hook-
225 and-line sampling due to their comparatively low density. Nets were set overnight (10–12 h) in
226 littoral, profundal, and pelagic habitats in each lake, except shallow full littoral lakes that lack pelagic
227 and profundal zones. All these principal habitats were sampled for at least three nights. Fish were
228 removed from nets, euthanized by cerebral concussion causing an immediate death and placed on
229 ice during transport to the laboratory.

230 All fish were identified to species and total length (± 1 mm) and age were determined. For
231 whitefish and vendace, the first left gill arch was dissected and the number of gill rakers counted for
232 morph and species identification purposes (Kahilainen et al., 2011a, b). In this region, whitefish may
233 occur as sympatric morphs having different number of gill rakers, diet, growth, and muscle THg
234 concentrations (Kahilainen and Østbye, 2006; Harrod et al., 2010; Kahilainen et al., 2017). In the
235 study lakes, whitefish occur as a single generalist morph, except Lake Ropi where we selected only

the littoral morph for this study (Hayden et al., 2013). Fish ages were determined using the most reliable hard structures for each species including burned cross-sections of otoliths, bones, and scales pressed on polycarbonate plates (Thomas et al., 2016). Two hard structures were simultaneously used to improve the aging accuracy (Kahilainen et al., 2017). Aging of pike was done using cleithrum bone and scale impressions. For perch operculum bone and burned cross-sections of otoliths were used, while for the other species (whitefish, vendace, roach, ruffe) clear and burned cross-sections of otoliths as well as scale impressions were used (Kahilainen et al., 2003, 2011b; Hayden et al., 2014a, 2015). Dorsal muscle tissue samples were taken from each sample, frozen at -20°C , freeze-dried for 48 hours, and grinded with glass rod to fine powder for THg analyses.

2.4. Total mercury analyses

Total mercury (THg) concentrations ($\mu\text{g g}^{-1}$ dry mass) were obtained using a Direct Mercury Analyser (Milestone DMA 80). Two replicates of each sample were analyzed to assess sample variability. A blank control and certified reference material (DORM-4) with known THg concentration (mean \pm SD, $0.410\pm0.055 \mu\text{g g}^{-1}$) were included at the beginning and end of each analytical run (mean \pm SD, $0.404\pm0.019 \mu\text{g g}^{-1}$, mean recovery 98.6 %, $n=390$). The THg concentration of each sample used in statistical analyses was derived by calculating the mean value of duplicates after subtracting the mean blank control values (mean \pm SD, $0.002\pm0.001 \mu\text{g g}^{-1}$, $n=390$). The mean of the duplicates for each sample was accepted for subsequent analyses only when the relative standard deviation (RSD) was less than 10 %. A randomized subset of 30 individuals was chosen from populations where sample size was greater than 30 to make systems comparable.

Due to a strong positive relationship between THg concentration and fish length/age, THg concentrations of fish were corrected for length/age prior to conducting inter-population comparisons (Sonesten, 2003a; Braaten et al., 2017). We first developed linear regression equations

for fish THg and length/age of each species in each lake (Table S4–5, Fig. S1–12). The equations were solved for the mean length and age of each species, resulting in a single mean length- and age-corrected THg value for each species within each lake (the average length and age of each species calculated from all studied lakes; Table 2) (Braaten et al., 2017). In populations where the relationship between THg and length or age was below statistically significant level, the length- and age-adjusted values were obtained by calculating the mean of the species-specific THg concentrations near mean length (± 2.5 cm) and age (± 1.5 years). Length- and age-adjusted THg concentrations were used for all subsequent statistical analyses examining population level differences.

2.5. Statistical analyses

Collinearity among environmental variables was first tested with linear regression analyses, and variables with $r^2 < 0.70$ were chosen for the further analyses. Principal component analysis (PCA) was used for the remaining variables to receive PC score for each study lake along environmental gradients using PC components. PC components explaining $>10\%$ of the variation were considered relevant for further evaluation of trends with THg concentrations and bioaccumulation rates. Lake PC scores were negative transformed ($*-1$) for THg analyses, because their connections to warmer climate and increased lake productivity were visually clearer compared to original scores (for original PC scores, see Table 1, Fig. 2).

Statistical testing of Hypothesis 1: Linear regression analysis was used to test the relationship between length- or age-adjusted THg concentration and lake PC scores. Lake-specific populations of each species were used for regression analyses only if the sample size was greater or equal to six.

Statistical testing of Hypothesis 2: The relationship between THg bioaccumulation rate (i.e. the slopes of significant linear regressions between THg, and length or age) and lake PC scores

284 representing different environmental gradients were also tested using simple linear regression
285 analysis. In addition, non-linear quadratic models were tested for species having visually non-linear
286 relationship between PC scores and THg bioaccumulation rate. Only populations with significant
287 bioaccumulation of THg relative to length or age could be chosen for the subsequent analyses of the
288 bioaccumulation rate.

289 The statistical significance limit to reject the null hypothesis (α) was 0.05 for all analyses.
290 Adjusted R-squared ($\text{adj.}r^2$) values were used for interpreting the significant results. For simplicity,
291 term r^2 is used in tables. All analyses were conducted using SPSS Statistics 24 (IBM Corp., Armonk,
292 NY, U.S.A.) or R (R Core Team, 2017).

293

294 3. RESULTS

295 3.1. *Environment, lake morphometry and catchment variation*

296 The collinearity of environmental variables was considerable due to their nature, and thus we
297 used the remaining 14 variables in PCA (Table 1; see the excluded variables in Table S1). The first
298 three PC components explained a total of 84 % of the variation among lakes (Fig. 2). PC1 explained
299 52 % of the variation and included variables related to climate and lake productivity (i.e. altitude,
300 air temperature, precipitation, total phosphorus, and compensation depth) and to catchment
301 related variables (i.e. forest percentage, ditch length and tree volume in the catchment area; see
302 loadings in the supplementary Table S2). PC1 lake scores were correlating negatively to lake climate-
303 productivity (Fig. 2, Table 1). The second axis (PC2) explained 19 % of the variance, represented
304 mainly lake morphometric characteristics (i.e. mean depth, lake volume, lake and catchment areas,
305 wetland proportion in catchment, see Table S2) and was negatively correlated with lake size (Fig. 2,
306 Table 1). The third axis (PC3) explained 13 % of the variance in lakes including catchment properties
307 (e.g. catchment-lake ratio and catchment area, as well as ditch length, wetland, and tree

308 proportions in catchment with much lower importance, see Table S2) with values correlating
309 negatively to catchment magnitude (Fig. 2, Table 1). Please note, that negative transformed values
310 ($*-1$) were used for lake scores for the subsequent analyses of the relationship between THg
311 concentration or THg bioaccumulation rate, and PC factors.

312

313 *3.2. Hypothesis 1: Connection between THg concentrations and lake PC scores*

314 Fish sample sizes were highly variable within species and lakes, partially due to differing
315 distribution limits of each species (Table 2). Whitefish and pike inhabited almost all the study lakes,
316 while other species were absent in the northernmost lakes. THg concentrations varied substantially
317 within species, the highest length- and age-adjusted THg concentrations being found in pike,
318 followed by perch and roach, and the lowest in vendace, ruffe, and whitefish (Table 2).
319 Bioaccumulation of THg relative to length and age varied substantially among fish species (Table S4–
320 5, Fig. S1–12). THg bioaccumulation relative to length and age were significant for vendace, perch,
321 pike, and ruffe in all or nearly all of the lakes, whereas whitefish and roach had significant regression
322 coefficients in approximately half of the cases (Table S4–5 and Fig. S1–12). Significant coefficients
323 were positive for all the species, except for whitefish having a significant negative relationship
324 between THg concentration and length in two northernmost lakes (Fig. S1).

325 Lake-specific length- and age-adjusted THg concentrations displayed statistically significant
326 relationships with PC1 (climate-productivity), but were unrelated to either PC2 (lake morphometry)
327 or PC3 (catchment magnitude; see Tables 3 and Table S3, Fig. 3 and Fig. S13–14). Length-adjusted
328 THg had a significant positive relationship with lake PC1 score for perch ($\text{adj.}r^2=0.50$, $p<0.01$), pike
329 ($\text{adj.}r^2=0.29$, $p<0.05$) and roach ($\text{adj.}r^2=0.57$, $p=0.05$), whereas relations were below statistically
330 significant levels for whitefish, ruffe and vendace. Significant positive relationships between age-
331 adjusted THg concentration and PC1 were found for vendace ($\text{adj.}r^2=0.50$, $p<0.05$), perch

332 (adj. r^2 =0.51, p <0.01), pike (adj. r^2 =0.55, p <0.005) and roach (adj. r^2 =0.61, p <0.05), while linear
333 models for whitefish and ruffe were non-significant (Table 3).

334
335 *3.3. Hypothesis 2: Bioaccumulation rate of THg relative to lake PC scores*

336 Bioaccumulation rate of THg relative to length or age (the slope of linear regression for each
337 lake and species, see Table S4–5) showed significant relationships with lake PC1 and PC3 scores, but
338 not with PC2 scores (Table 3, Fig. 3, Table S3, Fig. S13–14). Due to low number of populations having
339 statistically significant bioaccumulation of THg relative to length (n =3) or age (n =4), roach was
340 omitted from these analyses.

341 The bioaccumulation rate of whitefish THg relative to length displayed a positive linear
342 relationship with PC1 (adj. r^2 =0.34, p <0.05) (Table 3, Fig. 3). Non-linear u-shaped relationships were
343 found for perch (adj. r^2 =0.73; p <0.005) and ruffe (adj. r^2 =0.50, p <0.05). In addition, positive linear
344 relationships for vendace and pike were near the significance limit (vendace adj. r^2 =0.28, p =0.067;
345 pike adj. r^2 =0.22 p =0.052). THg bioaccumulation rate relative to age displayed a positive linear
346 relationship with PC1 for whitefish (adj. r^2 =0.72, p <0.005) and pike (adj. r^2 =0.40, p <0.01). A non-linear
347 relationship between THg bioaccumulation rate relative to age and PC1 was evident for perch
348 (adj. r^2 =0.64, p <0.005) and ruffe (adj. r^2 =0.50, p <0.05) (Table 3, Fig. 3). For vendace, the linear
349 relationship was close to being considered significant at the p = 0.05 level (adj. r^2 =0.41, p =0.053).

350 Bioaccumulation rate of THg relative to length for vendace (adj. r^2 =0.50, p <0.05) and perch
351 (adj. r^2 =0.55, p <0.01), and relative to age for pike (adj. r^2 =0.23, p <0.05) (Table 3, Fig. S14) were
352 positively related to lake PC3 score. Moreover, the relationship of PC3 with the bioaccumulation
353 rate relative to age was near the significance limit for vendace (adj. r^2 =0.32, p =0.085) and perch
354 (adj. r^2 =0.23, p =0.066), as well as relative to length for pike (adj. r^2 =0.22, p =0.054).

355

356 4. DISCUSSION

357 4.1. *Main results*

358 Increased THg tissue concentration was found in lakes of warmer climate and increased
359 productivity for most species. Adjusted tissue THg concentrations had significant and steep positive
360 slopes with lake climate-productivity (PC1) for perch and pike. Shallower, but still significant, slopes
361 were observed for vendace and roach, whilst no significant relationships were found for whitefish
362 and ruffe. An increasing THg bioaccumulation rate from north to south was not as robustly
363 supported statistically for warmer and more productive lakes. However, our results showed
364 significant positive slopes between THg bioaccumulation rate and PC1 for whitefish and pike, as well
365 as u-shaped relationships for perch and ruffe. Higher THg bioaccumulation rates were related to
366 increasing catchment magnitude (PC3) for vendace, perch, and pike, whereas no relationship
367 between THg concentration or bioaccumulation rate and lake morphometry (PC2) was found for
368 any species.

369

370 4.2. *THg concentration links to warming and eutrophication of Subarctic lakes*

371 Combined effects of changing climate-productivity and catchment land use in the Subarctic
372 study lakes was correlated with significantly elevated THg concentrations of several fish species.
373 Foraging guilds of our study fish species encompassed the full suite of foraging strategies evident in
374 these systems, ranging from top predator pike and mesopredator large perch to pelagic
375 zooplanktivore vendace and small roach and perch, as well as benthic invertivores whitefish and
376 ruffe. The highest increase in THg concentrations (i.e. the slope of the regression between THg and
377 PC1) along the study gradient were found for pike (length: 0.108; age: 0.104) and perch (length:
378 0.126; age: 0.102), whereas lower increases were found for vendace (age: 0.078) and roach (length:
379 0.093; age: 0.083). Moreover, ruffe and whitefish were lacking significant trends. Previous studies

380 have shown that higher THg levels in fish are connected to increasing trophic level of fish (e.g.
381 Jernelöv and Lann, 1971; Lavoie et al., 2013), as well as the reliance on pelagic rather than littoral
382 benthic food web (Power et al. 2002; Thomas et al., 2016; Kahilainen et al., 2017). Thus, the foraging
383 habitat and the trophic level of species likely influenced the observed trends in the mercury
384 concentrations.

385 The eutrophication trend of the study lakes, seen as increasing phosphorus and nitrogen
386 concentration and decreasing compensation depth, is evidently caused by joint effects of increasing
387 temperature and precipitation together with intensifying forestry practices, i.e. clear cutting, site
388 preparation and ditching (Jussila et al., 2014), while the proportion of agriculture in the catchments
389 is very low (<1 %). The ultimate source of eutrophication is likely important as sewage and
390 agriculture related eutrophication usually cause dilution of THg in fish muscle, whereas forestry
391 related eutrophication seems to have opposite effect (Sonesten, 2003b). Advancing spring thaw due
392 to temperature rise together with increasing precipitation and human-modified catchments
393 enhance the mobility of organic carbon and direct leaching of DOC and Hg to lakes (Stern et al.,
394 2012). The combination of warming lakes and increasing decomposition of DOC enhance low-
395 oxygen conditions suitable for bacterial methylation of Hg in both terrestrial and lake ecosystems
396 (Evans et al., 2005a, b; Lehnher, 2014; Yang et al., 2016). Over six-fold decrease in compensation
397 depth from north to lower latitudes likely relates to decreasing oxygen levels and elevating Hg
398 methylation activity.

399 The proportion of forested watershed (from 2 to 16 %) and artificial ditch kilometers (from 0 to
400 6.67 km/km²) in the lake catchment both increase towards lower latitudes with simultaneously
401 increasing THg concentrations of four out of six fish species studied. Despite the increasing forested
402 proportion and ditching length, the increase of tree volume (m³ ha⁻¹) in the catchment stopped
403 below the mesotrophic study lakes, and has decreased due to extensive clear-cuts in the southern

limits of the study region (Jussila et al., 2014). These trends strongly suggest a positive connection between land-use and Hg concentrations in fish. Previous studies have shown that forested peatland catchments and intensified forestry elevate THg concentrations in lake communities and fish (Sonesten, 2003b; Garcia and Carignan, 2005). Forested watersheds and forestry practices increase the load of nutrients, organic matter and Hg to lakes, as well as elevate Hg methylation both in the catchment and lakes (Porvari et al., 2003; Skyllberg et al., 2009; Kronberg et al., 2016a, b). Such effects of increasing direct leaching of Hg, as well as higher methylation activity due to decomposition of DOC have likely contributed to the increasing fish THg concentrations in our study lakes. The effects of forestry practices on THg in the water and biota are also highly dependent on the forestry operation methods, the cutting season, morphometric characteristics (e.g. slope) of the catchment area, and type of bedrock, complicating the development of robust forestry and water THg concentration relationships at the landscape level (Rask et al., 1998; Eklöf et al., 2014; Kronberg et al., 2016a; Ukonmaanaho et al., 2016).

In addition to direct leaching of mercury from clear-cut sites, it is likely that increasing temperature and productivity cause a shift in basal energy sources and have a role in elevated fish THg concentrations. Here, benthic-driven primary production typically dominates in cold oligotrophic lakes, where the pelagic zooplankton have only a single short peak during the mid to late summer (Kahilainen et al., 2003, 2005; Hayden et al., 2014b). In warmer and more productive lakes, the proportion of benthic primary production decreased along as a function of shading and nutrient competition by pelagic phytoplankton and bacterial production (Vadeboncoeur et al., 2003; Karlsson et al., 2009). Such effect is evident also in our lakes, where compensation depth decreased from 10 m in the northernmost lakes to 1.5 m in the southernmost lakes with a simultaneous increase in nutrient levels. Previous studies have found much higher THg concentrations in pelagic fish than benthic fish in Subarctic lakes (Power et al., 2002; Thomas et al., 2016; Kahilainen et al.,

2017). In the Subarctic lakes, littoral benthic macroinvertebrates have generally lower mercury content than zooplankton explaining the low THg concentration in benthivorous fish, such as whitefish and ruffe in the study lakes (Kahilainen et al., 2016, 2017; Keva et al., 2017). Zooplanktivores, such as vendace, small roach, and perch, as well as piscivorous fish (pike, large perch) feeding on these pelagic forage fish are often THg enriched (Thomas et al., 2016). However, these foraging guild related THg concentrations are not directly correlated with trends in bioaccumulation rates.

4.3. Links between THg bioaccumulation rate and climate-productivity

THg bioaccumulation rate (the slope of regression between THg and length or age) of whitefish and pike displayed a positive linear relationship with climate-productivity of lakes. However, u-shaped, non-linear relationships were observed for perch and ruffe, with the lowest THg bioaccumulation rate in the mesotrophic lakes. Changes in the THg bioaccumulation rate are less straight-forward than what was seen with THg concentrations, due to shifts in energy source towards pelagic and fish community structure along the lake gradient (Vadeboncouer et al. 2003; Thomas et al., 2016; Hayden et al., 2017).

For whitefish, THg bioaccumulation relative to length was negative in the northernmost lakes, whereas in more productive lakes bioaccumulation was positive. This change in the direction of the regression resulted in a positive relationship between bioaccumulation rate and lake climate-productivity in the full data. The increasing THg bioaccumulation rate of whitefish southward the climate-productivity gradient is likely related to changes in foraging habitats. In the northernmost oligotrophic lakes, whitefish use pelagic zooplankton mainly in juvenile phase and typically shift to littoral benthic invertebrates in later life stages (Kahilainen et al., 2003). Such ontogenetic diet shifts from THg rich pelagic zooplankton towards THg poor littoral benthic macroinvertebrates evidently

452 reduces the bioaccumulation rate of mercury (Kahilainen et al., 2017). However, whitefish
453 populations in the southern lakes do not demonstrate this ontogenetic shift and continue to feed
454 upon pelagic zooplankton (Heikinheimo et al., 2000), and this ontogenetic change in foraging
455 habitats could be seen in the changing bioaccumulation trends along our study lakes.

456 THg bioaccumulation rate is increasing for pike in the studied lake gradient from north to south,
457 which is probably related to changes in prey species composition in lower trophic levels, seen as a
458 shift in fish dominance from salmonids to percids and cyprinids toward lower latitudes (Hayden et
459 al., 2017). Pike and other piscivorous fish usually consume the most abundant and easily available
460 prey fish in Subarctic lakes (Kahilainen and Lehtonen 2003). A diet shift of pike and large perch from
461 benthivorous whitefish with relatively low and stable THg concentrations (Hayden et al., 2013;
462 Hayden et al. 2014a; Kahilainen et al., 2017) to other species such as perch, vendace or roach that
463 have increasing THg concentrations from north to south, would likely increase THg bioaccumulation
464 rate of piscivorous pike as well as large perch. Furthermore, larger individuals of aforementioned
465 prey species contained higher THg concentrations that is also important, as prey size of piscivores
466 generally increases with length (Kahilainen and Lehtonen, 2003). Increasing food-chain length
467 towards warmer and eutrophic lakes due to additional pelagic species in lower latitudes (Hayden et
468 al., 2014b; Thomas et al. 2016; Hayden et al., 2017) would also contribute to the higher THg
469 bioaccumulation rate especially in apex predators (pike and large perch).

470 Vendace, perch, and ruffe did not show evidence of significant linear relationships between THg
471 bioaccumulation rate and lake climate-productivity. However, data revealed u-shaped non-linear
472 relationships for perch and ruffe, with lowest bioaccumulation rate in the mesotrophic lakes. THg
473 concentrations of most fish species increased toward warmer and eutrophic lakes, but the rate of
474 THg bioaccumulation relative to length and age should not be affected, if the growth rate and the
475 THg levels of prey items remained stable. In addition, within the climate and productivity gradients

476 from north to south in the study region, a slight increase in temperature and productivity to a
477 moderate level may increase the growth rate of the study species and lead to growth dilution of THg
478 in fish muscle (Simoneau et al., 2005; Hayden et al., 2014a, 2017). This phenomenon is likely
479 responsible for the u-shaped relationships observed for perch and ruffe.

480 Positive relationships between THg bioaccumulation rate and catchment magnitude (PC3),
481 referring principally to the size of the catchment, were significant for vendace, perch, and pike.
482 However, PC3 axis explained only 13 %, of the variation between lakes, considerably less than either
483 PC1 or PC2. Moreover, the PC3 score of Lake Vaatto (lake number 17 in Fig. 1), a large and
484 completely ditched catchment, is clearly different from the other lakes and likely driving significant
485 relationships for the fish species. Since all the other lakes are rather similar with regard to the
486 relative catchment size, caution should be taken when interpreting any possible relationship
487 between PC3 scores and THg bioaccumulation rate, despite the statistically significant regression.

488

489 4.4. Human health considerations

490 High mercury exposure to humans has been linked to damage in neurological, reproductive,
491 immune, and cardiovascular systems (Mergler et al., 2007). The maximum acceptable level set by
492 United Nations (Codex Alimentarius, 1995) of THg in fish muscle tissue for human diet is $0.5 \mu\text{g g}^{-1}$
493 wet mass for non-piscivorous fish (all study species except pike) and $1 \mu\text{g g}^{-1}$ for predatory fish (e.g.
494 pike) that corresponds to approximately $2.5\text{--}5 \mu\text{g g}^{-1}$ dry mass. Most of the fish species sampled in
495 this current study had THg concentrations below these international health limits, except for a few
496 individual predator perch ($n=4$) and pike ($n=4$). The fish with the highest THg concentrations were
497 typically large, old, and located in the most eutrophic and warmest lakes. Thus, local people
498 consuming fishes in the southern lakes, especially pike and perch that are target species of
499 subsistence and recreational fishing, have a higher risk of exposure to THg relative to people

500 consuming fishes caught in northern lakes, where whitefish is the target species (Thomas et al.,
501 2016; Kahilainen et al., 2017; Keva et al., 2017). More attention should also be paid to the fact, that
502 fish consumption in the Arctic and Subarctic, e.g. by indigenous Sami people, is generally higher than
503 in lower latitudes and most of the consumption is locally derived fish (Sjölander, 2011). Generally,
504 the increasing THg concentrations of important subsistence fishery species (vendace, perch, and
505 pike) along the climate-productivity gradient of this study from north to south, adds further
506 evidence of adverse effects of eutrophication on the quality of fish as a human diet resource (Taipale
507 et al., 2016).

508

509 5. CONCLUSIONS

510 This study revealed a positive linear relationship between adjusted THg concentration in fish and
511 increasing climate-productivity values of Subarctic lakes for several fish species. Results indicated
512 that lake eutrophication due to climatic change and intensification of forestry related land use
513 activities have joint effects, elevating THg concentrations in several fish species. Accelerating THg
514 bioaccumulation rate towards warmer and more productive lakes was evident for whitefish and
515 pike, whereas a u-shaped relationship was found for perch and ruffe, indicating that a minor
516 increase in lake temperature and trophic state might lead to growth dilution of Hg for some fish
517 species, whereas loss of clarity and eutrophication lead to elevated THg burden. As evident in the
518 study, THg bioaccumulation and dynamics are both species-specific and lake-specific, and thus the
519 results should be interpreted along the full lake gradient from north to south for each species.
520 Combined effects of climate and land use are highly complex, altering both abiotic and biotic factors
521 in each lake and catchment, and need to be considered in future THg studies of fish. Generally, there
522 is evident need for future studies that examine entire food webs, revealing the pelagic and benthic
523 contributions of THg sources and subsequent biomagnification patterns along climatic and

524 productivity gradients. Such baseline studies are critical for a selection of lakes in the long-term
525 monitoring studies of THg concentrations in the rapidly changing Subarctic.

526

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534

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751

752 TABLES

753

754 *Table 1.* Study lakes and selected environmental variables used in principal component analyses (PCA). Altitude (Alt), mean precipitation (Precip)
755 and air temperature (Air temp) in open-water season (June–September 1981–2010), total phosphorus (TP), compensation (Comp) and mean
756 (Mean) depths, lake volume (LV), lake area (LA), catchment area (CA), forest (For) and wetland (Wet) percentages in the catchment area, ditching
757 length (km) per 1 km² of catchment area (Ditch), tree volume (TV) per hectare of forested and wetland area, catchment-lake area ratio (CA:LA).
758 PCA scores for each lake representing climate and productivity (PC1), lake morphometry (PC2), and catchment magnitude (PC3). Please note that
759 lakes (column No) are ordered by PC1 scores.

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No	Lake	Alt (m a.s.l)	Precip (mm)	Air temp (°C)	TP (µg/L)	Depth (m) Comp	Mean	LV (milj m ³)	LA (km ²)	CA (km ²)	For (%)	Wet (%)	Ditch (km/km ²)	TV (m ³ /ha)	CA:LA	PC1 (52%)	PC2 (19%)	PC3 (13%)
1	Kilpis	473	197	8.4	4	10	19.4	728.0	37.3	260.35	8.90	4.09	0	18.66	6.98	4.91	-5.62	-0.54
2	Tsahkal	559	197	8.4	5	7.5	9	10.1	1.1	28.76	2.00	5.28	0	7.01	26.15	3.77	0.63	0.16
3	Kolta	490	197	8.4	3	9	1.1	1.4	1.3	31.04	6.90	4.00	0	13.04	23.88	3.33	1.33	0.22
4	Kuohkima	489	197	8.4	3	8	2.6	0.8	0.3	36.17	7.10	2.60	0	12.39	120.58	3.18	1.35	-0.84
5	Oiko	448	218	8.7	7	5	3.1	3.7	1.2	21.24	19.90	10.15	0	20.15	17.70	2.02	1.20	0.46
6	Kivi	445	221	8.7	7	5	2.8	9.7	3.5	165.03	4.70	15.88	0	24.23	47.15	1.99	1.11	-0.60
7	Ropi	399	240	9	10	5	6.9	8.9	1.3	86.80	12.89	18.18	0	23.96	66.77	1.52	0.84	-0.40
8	Palo	346	224	9.4	21	3	0.8	3.0	3.5	134.44	31.50	32.24	0.01	23.29	38.41	0.38	1.56	-0.37
9	Vaggoval	331	236	9.8	12	4	0.5	0.8	1.8	6.03	36.03	38.99	0	32.58	3.35	0.26	1.89	0.53
10	Äkäs	263	256	10.5	18	4.5	3	39.1	13.1	74.04	56.13	12.66	0.15	81.78	5.65	-1.08	-0.54	1.01
11	Jeris	258	256	10.5	25	3.5	3.4	80.8	23.5	98.84	56.02	8.16	0.20	76.11	4.21	-1.19	-1.48	1.07
12	Toras	247	256	10.4	18	3.5	3	14.7	4.9	215.34	62.30	9.90	0.14	80.55	43.95	-1.47	-0.17	-0.05
13	Särki	261	256	10.5	25	1.5	5.1	26.0	5	14.71	58.21	4.68	0.49	74.77	2.94	-1.51	-0.30	1.37
14	Särkilompolo	255	256	10.5	36	2.5	3.7	4.7	1.3	36.93	68.96	6.57	0.23	74.20	28.41	-1.91	0.06	1.05
15	Aalis	177	257	11.4	45	1.5	3.2	19.3	6	72.25	62.25	12.55	6.67	71.09	12.04	-3.35	-0.50	0.58
16	Pasma	164	257	11.3	48	1.5	1.6	13.0	8.4	134.63	65.03	10.59	5.70	71.45	16.03	-3.45	-0.57	0.41
17	Vaatto	156	257	11.2	30	1.5	1.8	4.2	2.3	637.97	65.03	17.28	5.62	70.45	277.38	-3.62	-0.24	-4.96
18	Rattos	118	257	11.6	47	1.5	2.1	8.6	4.1	58.06	72.96	4.27	5.65	78.60	14.16	-3.77	-0.54	0.89

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770 *Table 2.* Sample sizes (n) and mean, length- and age-adjusted THg concentrations ($\mu\text{g g}^{-1}$ dry weight) for whitefish (mean length: 23.4 cm, mean
771 age: 4.7 years, n=467), vendace (mean length: 13.6 cm, mean age: 3.2 years, n=283), perch (mean length: 16.4 cm, mean age: 4.6 years, n=361),
772 pike (mean length: 50.4 cm, mean age: 6.2 years, n=312), roach (mean length: 14.1 cm, mean age: 6.2 years, n=193) and ruffe (mean length: 9.6
773 cm, mean age: 4.1 years, n=409) for each lake. Absence of fish species in the lake is marked as A. Three highest species-specific THg-
774 concentrations for each lake are bolded. Please note that lakes (column No) are ordered by PC1 scores.

No Lake		Whitefish THg					Vendace THg					Perch THg					Pike THg					Roach THg					Ruffe THg				
		n	mean	length	age	n	mean	length	age	n	mean	length	age	n	mean	length	age	n	mean	length	age	n	mean	length	Age						
1	Kilpis	30	0.16	0.19	0.20	A	–	–	–	A	–	–	–	30	0.65	0.49	0.59	A	–	–	–	A	–	–	–						
2	Tsahkal	30	0.43	0.39	0.48	A	–	–	–	A	–	–	–	A	–	–	–	A	–	–	–	A	–	–	–						
3	Kolta	30	0.18	0.17	0.18	A	–	–	–	A	–	–	–	16	0.59	0.72	0.64	A	–	–	–	A	–	–	–						
4	Kuohkima	30	0.36	0.34	0.31	A	–	–	–	A	–	–	–	18	0.99	–	–	A	–	–	–	A	–	–	–						
5	Oiko	30	0.47	0.46	0.47	A	–	–	–	A	–	–	–	27	1.68	1.66	1.56	1	–	–	–	30	0.40	0.34	0.35						
6	Kivi	30	0.40	0.45	0.39	A	–	–	–	30	0.80	0.36	0.31	18	1.64	1.37	1.22	A	–	–	–	30	0.60	0.57	0.44						
7	Ropi	30	0.22	0.23	0.21	A	–	–	–	2	0.30	–	–	22	0.51	0.76	0.85	1	–	–	–	21	0.51	0.53	0.44						
8	Palo	30	0.23	0.17	0.22	30	0.24	0.19	0.29	30	0.27	0.26	0.29	15	0.60	0.63	0.76	5	0.30	–	–	30	0.21	0.21	0.27						
9	Vaggoval	30	0.24	0.26	0.37	A	–	–	–	30	0.33	0.34	0.44	27	0.72	0.90	0.89	1	–	–	–	28	0.52	0.52	0.52						
10	Äkäs	30	0.17	0.34	0.17	30	0.28	0.29	0.29	30	0.29	0.28	0.36	6	0.78	0.75	1.00	30	0.21	0.23	0.21	30	0.17	0.12	0.17						
11	Jeris	30	0.20	0.20	0.27	30	0.26	0.27	0.24	30	0.25	0.31	0.43	4	0.47	–	–	A	–	–	–	30	0.22	0.21	0.25						
12	Toras	30	0.23	0.21	0.25	30	0.28	0.30	0.32	30	0.31	0.35	0.38	3	0.82	–	–	30	0.42	0.40	0.41	30	0.35	0.32	0.36						
13	Särki	30	0.21	0.19	0.24	30	0.18	0.17	0.17	30	0.22	0.24	0.20	1	–	–	–	A	–	–	–	30	0.15	0.11	0.16						
14	Särkilompolo	30	0.16	0.14	0.15	30	0.54	0.59	0.40	30	0.30	0.33	0.31	17	1.20	1.24	1.31	5	0.33	–	0.32	30	0.07	0.08	0.11						
15	Aalis	A	–	–	–	30	0.46	0.57	0.45	29	0.75	0.78	0.76	30	1.81	1.09	1.62	30	0.37	0.37	0.38	30	0.55	0.60	0.56						
16	Pasma	30	0.27	0.26	0.35	30	0.35	0.30	0.36	30	0.59	0.61	0.60	24	2.17	1.81	1.44	30	0.42	0.49	0.44	30	0.27	0.36	0.32						
17	Vaatto	14	0.45	0.46	0.48	13	0.49	0.21	0.64	30	1.03	1.07	0.91	28	2.36	2.36	1.81	30	0.56	0.58	0.54	30	0.48	0.55	0.43						
18	Rattos	3	0.26	–	–	30	0.47	0.68	0.57	30	1.01	1.08	0.92	26	1.64	1.57	1.56	30	0.60	0.59	0.53	30	0.39	0.57	0.40						

775 *Table 3.* Regression equations, adjusted R-squared (r^2), p-values and F-values with degrees of freedom for each species between lake-specific
776 length-/age-adjusted THg concentration ($\mu\text{g g}^{-1}$ dry weight), as well as accumulation rate (Slope) relative to length and age and PC1 and PC3
777 scores. Statistically significant ($p < 0.05$) models are bolded and marked with *. Roach was excluded from the analyses of THg accumulation rate
778 due to low sample size. Regressions for PC2 are found as supplementary material in Table S3.

779

Model	Whitefish	Vendace	Perch	Pike	Roach	Ruffe
THg (length) ~ PC1	$y = -0.004x + 0.276$; $r^2 = -0.06$; $p = 0.738$; $F_{1,14} = 0.12$	$y = 0.067x + 0.217$; $r^2 = 0.16$; $p = 0.135$; $F_{1,8} = 2.76$	$y = 0.126x + 0.304$; $r^2 = 0.50$; $p = 0.006$; $F_{1,10} = 12.01$	$y = 0.108x + 1.179$; $r^2 = 0.29$; $p = 0.026$; $F_{1,12} = 6.47$	$y = 0.093x + 0.183$; $r^2 = 0.57$; $p = 0.050$; $F_{1,4} = 7.68$	$y = 0.006x + 0.352$; $r^2 = -0.08$; $p = 0.831$; $F_{1,12} = 0.05$
THg (age) ~ PC1	$y = 0.000x + 0.296$; $r^2 = -0.07$; $p = 0.972$; $F_{1,14} = 0.00$	$y = 0.078x + 0.208$; $r^2 = 0.50$; $p = 0.014$; $F_{1,8} = 9.87$	$y = 0.102x + 0.332$; $r^2 = 0.51$; $p = 0.005$; $F_{1,10} = 12.53$	$y = 0.104x + 1.159$; $r^2 = 0.55$; $p = 0.002$; $F_{1,12} = 16.55$	$y = 0.083x + 0.182$; $r^2 = 0.61$; $p = 0.024$; $F_{1,5} = 10.25$	$y = 0.007x + 0.317$; $r^2 = -0.07$; $p = 0.703$; $F_{1,12} = 0.15$
Slope (length) ~ PC1	$y = 0.002x + 0.007$; $r^2 = 0.34$; $p = 0.046$; $F_{1,8} = 5.60$	$y = 0.017x + 0.011$; $r^2 = 0.28$; $p = 0.067$; $F_{1,8} = 4.50$	$y = 0.006x^2 - 0.008x + 0.02$; $r^2 = 0.73$; $p = 0.002$; $F_{2,8} = 14.3$	$y = 0.005x + 0.037$; $r^2 = 0.22$; $p = 0.052$; $F_{1,12} = 4.65$	–	$y = 0.005x^2 - 0.006x + 0.02$; $r^2 = 0.50$; $p = 0.018$; $F_{2,9} = 6.55$
Slope (age) ~ PC1	$y = 0.006x + 0.027$; $r^2 = 0.72$; $p = 0.002$; $F_{1,7} = 21.74$	$y = 0.024x + 0.029$; $r^2 = 0.41$; $p = 0.053$; $F_{1,6} = 5.78$	$y = 0.012x^2 - 0.012x + 0.05$; $r^2 = 0.64$; $p = 0.004$; $F_{2,9} = 10.7$	$y = 0.025x + 0.185$; $r^2 = 0.40$; $p = 0.009$; $F_{1,12} = 9.58$	–	$y = 0.004x^2 - 0.009x + 0.033$; $r^2 = 0.50$; $p = 0.018$; $F_{2,9} = 6.49$
THg (length) ~ PC3	$y = 0.036x + 0.274$; $r^2 = 0.17$; $p = 0.064$; $F_{1,14} = 4.03$	$y = -0.032x + 0.354$; $r^2 = -0.01$; $p = 0.356$; $F_{1,8} = 0.96$	$y = 0.094x + 0.508$; $r^2 = 0.19$; $p = 0.089$; $F_{1,10} = 3.56$	$y = 0.170x + 1.145$; $r^2 = 0.17$; $p = 0.080$; $F_{1,12} = 3.66$	$y = 0.030x + 0.433$; $r^2 = 0.05$; $p = 0.321$; $F_{1,4} = 1.28$	$y = 0.053x + 0.362$; $r^2 = 0.12$; $p = 0.120$; $F_{1,12} = 2.80$
THg (age) ~ PC3	$y = 0.035x + 0.293$; $r^2 = 0.14$; $p = 0.083$; $F_{1,14} = 3.48$	$y = 0.049x + 0.376$; $r^2 = 0.32$; $p = 0.051$; $F_{1,8} = 5.26$	$y = 0.067x + 0.496$; $r^2 = 0.13$; $p = 0.134$; $F_{1,10} = 2.66$	$y = 0.062x + 1.145$; $r^2 = -0.02$; $p = 0.420$; $F_{1,12} = 0.70$	$y = 0.030x + 0.399$; $r^2 = 0.17$; $p = 0.194$; $F_{1,5} = 2.25$	$y = 0.029x + 0.327$; $r^2 = 0.05$; $p = 0.221$; $F_{1,12} = 1.66$
Slope (length) ~ PC3	$y = 0.000x + 0.005$; $r^2 = -0.12$; $p = 0.855$; $F_{1,8} = 0.037$	$y = 0.016x + 0.047$; $r^2 = 0.50$; $p = 0.013$; $F_{1,8} = 10.0$	$y = 0.011x + 0.035$; $r^2 = 0.55$; $p = 0.005$; $F_{1,10} = 13.28$	$y = 0.009x + 0.036$; $r^2 = 0.22$; $p = 0.054$; $F_{1,12} = 4.56$	–	$y = 0.004x + 0.042$; $r^2 = -0.02$; $p = 0.407$; $F_{1,10} = 0.75$
Slope (age) ~ PC3	$y = 0.003x + 0.026$; $r^2 = -0.06$; $p = 0.480$; $F_{1,7} = 0.56$	$y = 0.016x + 0.079$; $r^2 = 0.32$; $p = 0.085$; $F_{1,6} = 4.24$	$y = 0.019x + 0.098$; $r^2 = 0.23$; $p = 0.066$; $F_{1,10} = 4.27$	$y = 0.038x + 0.177$; $r^2 = 0.23$; $p = 0.046$; $F_{1,12} = 4.95$	–	$y = 0.000x + 0.046$; $r^2 = -0.10$; $p = 0.905$; $F_{1,10} = 0.02$

780 FIGURE CAPTIONS

781

782 **Fig. 1.** The location of Tornio-Muoniojoki watercourse (mainstem forms a border between Finland
783 and Sweden) and tributary lakes 1–18 (a) in northern Fennoscandia (b). Lakes are numbered
784 according their PC1 scores. Asterisks indicate locations of six weather stations and their open-water
785 season (June–September 1981–2010) air temperature (°C) and precipitation (mm). Arrows are
786 flowing directions of rivers towards south and watercourse finally discharges to the northernmost
787 part of Baltic Sea. Solid lines indicate distribution limit of coniferous trees, where Norway spruce
788 border indicate the start of forestry practices. Mountain birch distribution covers the northernmost
789 lake catchments.

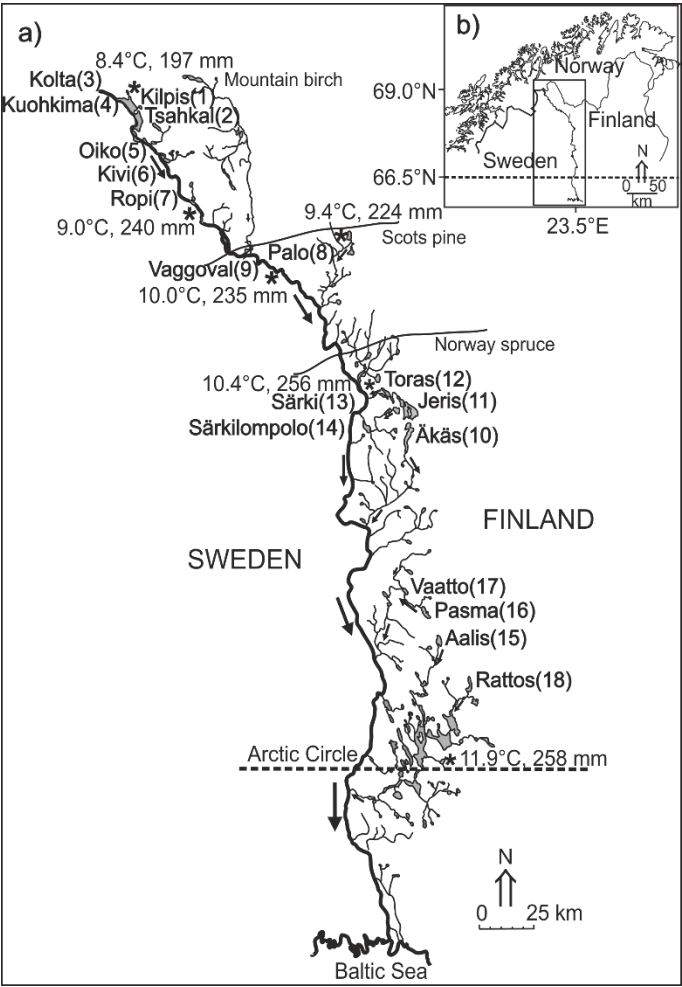
790

791 **Fig. 2.** Results of principal component analysis (PCA) representing the first three axes explaining
792 most of the variation (total 84 %) with a total of 14 environmental variables (Table 1) presented in
793 three bi-plots (a, b, c). The first axis (PC1) describes climate-productivity, the second axis (PC2) lake
794 morphometry, and the third axis (PC3) catchment magnitude. The arrow lengths indicate the
795 importance of an environmental variable. For lake scores, see Table 1 and for variable loadings, see
796 Table S2.

797

798 **Fig. 3.** The relationship between climate-productivity factor (PC1, for clarity opposite lake score
799 values are used) to species-specific length-adjusted THg concentrations (the topmost row) and age-
800 adjusted THg concentrations (the second row), as well as THg bioaccumulation rate relative to
801 length (the third row) and age (the fourth row). Please note that THg concentrations are indicated
802 as dry weight. The regression lines and 95 % confidence intervals are added only to statistically
803 significant ($p < 0.05$) cases. For regression equations, see Table 3.

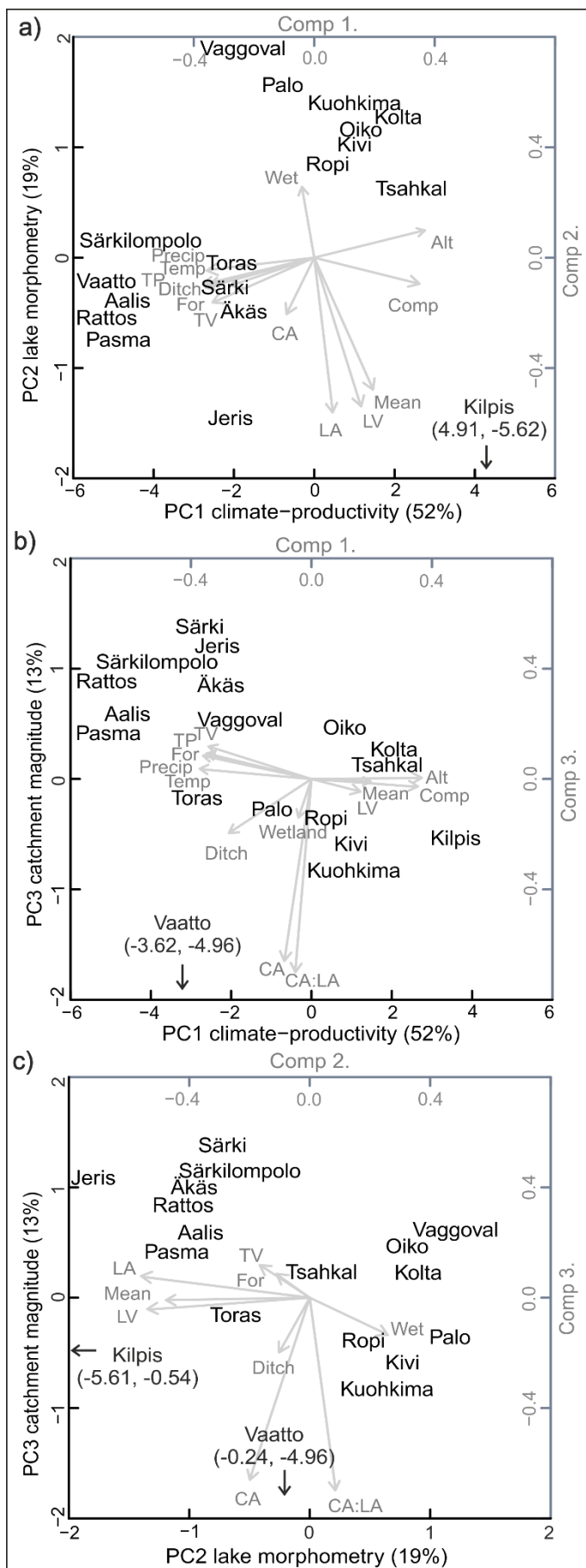
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806 Fig. 1

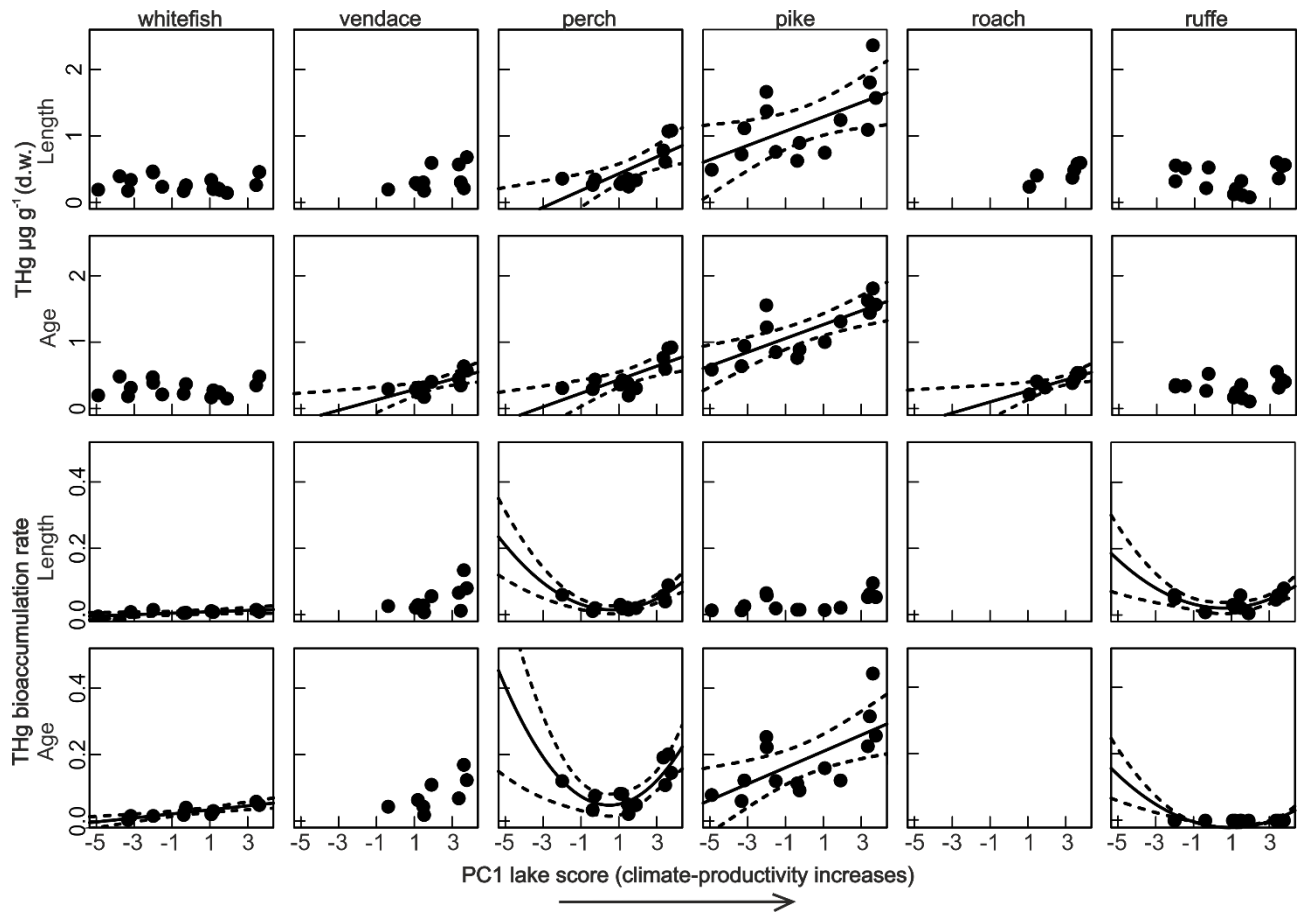
807



809 Fig. 2.

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813 Fig. 3.

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815 SUPPLEMENTARY INFORMATION

816 *Table S1.* Study lakes and environmental variables that were excluded from PCA-analysis due to collinearity. Latitude (Lat), longitude (Long), total
817 nitrogen (TN) maximum depth (Max depth), littoral portion of the lakes (Litt), the amount of fish species (Species), number of households (HH),
818 urban (Urban), agriculture, sparse vegetation and water percentages in the lake catchment. Please note that lakes (column No) are ordered by
819 PC1 scores.

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No	Lake	Lat (°N)	Long (°E)	TN (µg L ⁻¹)	Max depth (m)	Litt (%)	Species n	HH (km ²)	Urban (%)	Agriculture (%)	Sparse veg. (%)	Water (%)
1	Kilpis	69.03	20.49	120	57	29	8	7	0.71	0	70.64	15.65
2	Tsahkal	69.01	20.55	140	30	60	4	0	0	0	89.43	5.28
3	Kolta	69.03	20.30	97	3	100	6	2	0	0	79.10	10.00
4	Kuohkima	69.03	20.33	200	10	99	6	7	0	0	78.30	12.00
5	Oiko	68.50	21.13	215	10	84	9	3	0.19	0	61.99	7.76
6	Kivi	68.49	21.15	201	10	84	9	1	0	0	74.22	5.19
7	Ropi	68.41	21.35	273	20	54	11	11	0	0	65.43	3.49
8	Palo	68.34	23.21	470	2	100	8	11	0.42	0.10	31.39	4.33
9	Vaggoval	68.30	22.14	590	2.5	100	7	15	0.19	0	0.29	24.48
10	Akas	67.49	24.07	350	12	77	8	7	0.79	0.19	14.35	15.85
11	Jeris	67.55	24.06	550	12	59	9	15	1.49	0.39	9.45	24.47
12	Toras	67.58	23.52	600	8.5	51	10	7	0.90	0.20	9.20	17.5
13	Särki	67.54	23.58	520	14	14	6	18	2.18	0.19	9.25	25.47
14	Särkilompolo	67.54	23.54	420	8.3	30	8	45	1.39	0.09	8.35	14.62
15	Aalis	67.00	24.32	830	6	19	9	7	0.79	0.29	16.10	7.96
16	Pasma	67.07	24.22	1100	4.1	99	8	12	0.99	0.99	16.08	6.29
17	Vaatto	67.12	24.09	470	4.5	33	8	49	0.59	0.89	13.48	2.69
18	Rattos	66.50	24.52	520	6.8	32	8	21	0.99	0.69	13.61	7.45

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824 *Table S2.* Loadings of the 14 selected environmental variables in three first components of PCA analysis including Alt (altitude), Precip
825 (precipitation), Temp (temperature), TP (total phosphorus), Comp (compensation depth), Mean (mean depth), LV (lake volume), LA (lake area),
826 CA (catchment area), For (forested area of the catchment), Wet (wetland area of the catchment), Ditch (ditch kilometers per catchment area),
827 TV (tree volume in the catchment), and CA:LA (catchment-lake area ratio). The farther the value is from zero, the more significance it has in the
828 component. See Table 1 for units.

	Alt	Precip	Temp	TP	Comp	Mean	LV	LA	CA	For	Wet	Ditch	TV	CA:LA
Comp.1	0.36	−0.35	−0.36	−0.34	0.35	0.19	0.15	0.06	−0.09	−0.35	−0.04	−0.27	−0.33	−0.05
Comp.2	0.10	−0.04	−0.10	−0.09	−0.09	−0.47	−0.53	−0.55	−0.20	−0.11	0.25	−0.10	−0.16	0.09
Comp.3	0.00	0.08	0.04	0.09	−0.03	−0.01	−0.04	0.08	−0.65	0.08	−0.13	−0.19	0.11	−0.69

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831 *Table S3.* Regression equations, adjusted R-squared (r^2), p-values and F-values with degrees of freedom for each species between lake-specific
832 length-/age-adjusted THg concentration ($\mu\text{g g}^{-1}$ dry weight), as well as accumulation rate (Slope) relative to length and age and lake PC2 scores.
833 Statistically significant ($p < 0.05$) models are bolded. Roach was excluded from the analyses of THg accumulation rate due to low sample size.

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Model	Whitefish	Vendace	Perch	Pike	Roach	Ruffe
THg (length) ~ PC2	$y = -0.016x + 0.277$; $r^2 = -0.00$; $p = 0.340$; $F_{1,14} = 0.98$	$y = 0.042x + 0.346$; $r^2 = -0.09$; $p = 0.628$; $F_{1,8} = 0.25$	$y = 0.091x + 0.503$; $r^2 = -0.00$; $p = 0.359$; $F_{1,10} = 0.92$	$y = -0.036x + 1.172$; $r^2 = -0.07$; $p = 0.663$; $F_{1,12} = 0.20$	$y = -0.138x + 0.503$; $r^2 = -0.21$; $p = 0.740$; $F_{1,4} = 0.13$	$y = -0.042x + 0.351$; $r^2 = 0.03$; $p = 0.457$; $F_{1,12} = 0.59$
THg (age) ~ PC2	$y = -0.018x + 0.295$; $r^2 = 0.01$; $p = 0.298$; $F_{1,14} = 1.17$	$y = 0.001x + 0.371$; $r^2 = -0.13$; $p = 0.983$; $F_{1,8} = 0.00$	$y = 0.082x + 0.492$; $r^2 = 0.02$; $p = 0.299$; $F_{1,10} = 1.20$	$y = -0.016x + 1.155$; $r^2 = -0.08$; $p = 0.799$; $F_{1,12} = 0.07$	$y = 0.035x + 0.391$; $r^2 = -0.19$; $p = 0.877$; $F_{1,5} = 0.03$	$y = -0.032x + 0.319$; $r^2 = -0.02$; $p = 0.411$; $F_{1,12} = 0.73$
Slope (length) ~ PC2	$y = -0.001x + 0.006$; $r^2 = -0.06$; $p = 0.487$; $F_{1,8} = 0.53$	$y = 0.001x + 0.046$; $r^2 = -0.12$; $p = 0.943$; $F_{1,8} = 0.01$	$y = 0.003x + 0.035$; $r^2 = -0.10$; $p = 0.721$; $F_{1,9} = 0.14$	$y = 0.000x + 0.037$; $r^2 = -0.08$; $p = 0.913$; $F_{1,12} = 0.01$	–	$y = 0.003x + 0.041$; $r^2 = -0.09$; $p = 0.765$; $F_{1,10} = 0.09$
Slope (age) ~ PC2	$y = 0.007x + 0.03$; $r^2 = 0.08$; $p = 0.234$; $F_{1,7} = 1.70$	$y = 0.009x + 0.078$; $r^2 = -0.14$; $p = 0.721$; $F_{1,6} = 0.14$	$y = 0.015x + 0.097$; $r^2 = -0.03$; $p = 0.441$; $F_{1,10} = 0.64$	$y = 0.001x + 0.185$; $r^2 = -0.08$; $p = 0.946$; $F_{1,12} = 0.01$	–	$y = -0.003x + 0.046$; $r^2 = -0.09$; $p = 0.719$; $F_{1,10} = 0.14$

835 *Table S4.* Lake-specific linear regression equations, adjusted R-squared (r^2), p-values and F-values with degrees of freedom between THg
836 concentration ($\mu\text{g g}^{-1}$ dry weight) and fish total length (cm) for each species. Statistically significant ($p < 0.05$) equations are bolded. Please note
837 that lakes (column No) are ordered by PC1 scores.

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Lake	Whitefish	Vendace	Perch	Pike	Roach	Ruffe
1. Kilpis	$y = -0.005x + 0.306$; $r^2 = 0.26$; $p < 0.01$; $F_{1,28} = 11.08$	–	–	$y = 0.013x - 0.166$; $r^2 = 0.70$; $p < 0.001$; $F_{1,28} = 69.24$	–	–
2. Tsahkal	$y = -0.016x + 0.766$; $r^2 = 0.23$; $p < 0.01$; $F_{1,28} = 9.57$	–	–	–	–	–
3. Kolta	$y = 0.001x + 0.162$; $r^2 = 0.04$; $p = 0.138$; $F_{1,28} = 2.34$	–	–	$y = 0.013x + 0.066$; $r^2 = 0.81$; $p < 0.001$; $F_{1,14} = 66.50$	–	–
4. Kuohkima	$y = 0.008x + 0.149$; $r^2 = 0.21$; $p < 0.01$; $F_{1,28} = 8.64$	–	–	$y = 0.026x - 0.197$; $r^2 = 0.56$; $p < 0.001$; $F_{1,16} = 23.07$	–	–
5. Oiko	$y = 0.002x + 0.423$; $r^2 = 0.05$; $p = 0.239$; $F_{1,28} = 1.45$	–	–	$y = 0.065x - 1.616$; $r^2 = 0.70$; $p < 0.001$; $F_{1,25} = 62.77$	–	$y = 0.061x - 0.259$; $r^2 = 0.61$; $p < 0.001$; $F_{1,28} = 45.84$
6. Kivi	$y = 0.015x + 0.098$; $r^2 = 0.46$; $p < 0.001$; $F_{1,28} = 25.21$	–	$y = 0.060x - 0.626$; $r^2 = 0.58$; $p < 0.001$; $F_{1,28} = 41.23$	$y = 0.058x - 1.553$; $r^2 = 0.61$; $p < 0.001$; $F_{1,16} = 26.99$	–	$y = 0.049x + 0.085$; $r^2 = 0.19$; $p < 0.05$; $F_{1,28} = 7.73$
7. Ropi	$y = 0.005x + 0.107$; $r^2 = 0.01$; $p = 0.249$; $F_{1,28} = 1.39$	–	–	$y = 0.019x - 0.200$; $r^2 = 0.52$; $p < 0.001$; $F_{1,20} = 23.83$	–	$y = -0.031x + 0.810$; $r^2 = 0.06$; $p = 0.156$; $F_{1,19} = 2.18$
8. Palo	$y = 0.005x + 0.053$; $r^2 = 0.53$; $p < 0.001$; $F_{1,28} = 33.21$	$y = 0.026x - 0.162$; $r^2 = 0.72$; $p < 0.001$; $F_{1,28} = 74.53$	$y = 0.011x + 0.082$; $r^2 = 0.63$; $p < 0.001$; $F_{1,28} = 51.13$	$y = 0.015x - 0.132$; $r^2 = 0.82$; $p < 0.001$; $F_{1,13} = 66.37$	–	$y = 0.008x + 0.136$; $r^2 = 0.29$; $p < 0.005$; $F_{1,28} = 13.0$
9. Vaggoval	$y = 0.006x + 0.116$; $r^2 = 0.51$; $p < 0.001$; $F_{1,28} = 31.10$	–	$y = 0.020x + 0.016$; $r^2 = 0.64$; $p < 0.001$; $F_{1,28} = 52.28$	$y = 0.015x + 0.138$; $r^2 = 0.67$; $p < 0.001$; $F_{1,25} = 52.73$	–	$y = 0.010x + 0.430$; $r^2 = -0.04$; $p = 0.789$; $F_{1,26} = 0.07$
10. Äkäs	$y = 0.011x - 0.079$; $r^2 = 0.67$; $p < 0.001$; $F_{1,28} = 59.37$	$y = 0.021x + 0.005$; $r^2 = 0.20$; $p < 0.01$; $F_{1,28} = 8.00$	$y = 0.030x - 0.216$; $r^2 = 0.85$; $p < 0.001$; $F_{1,27} = 164.49$	$y = 0.014x + 0.040$; $r^2 = 0.81$; $p < 0.01$; $F_{1,4} = 22.50$	$y = -0.007x + 0.321$; $r^2 = 0.05$; $p = 0.132$; $F_{1,28} = 2.41$	$y = 0.030x - 0.167$; $r^2 = 0.72$; $p < 0.001$; $F_{1,28} = 76.90$
11. Jeris	$y = 0.008x + 0.012$; $r^2 = 0.42$; $p < 0.001$; $F_{1,28} = 21.83$	$y = 0.029x - 0.128$; $r^2 = 0.66$; $p < 0.001$; $F_{1,28} = 56.10$	$y = 0.020x - 0.002$; $r^2 = 0.50$; $p < 0.001$; $F_{1,25} = 26.83$	–	–	$y = 0.022x - 0.006$; $r^2 = 0.68$; $p < 0.001$; $F_{1,28} = 61.10$
12. Toras	$y = 0.001x + 0.217$; $r^2 = -0.02$; $p = 0.575$; $F_{1,28} = 0.32$	$y = 0.028x - 0.082$; $r^2 = 0.61$; $p < 0.001$; $F_{1,28} = 45.83$	$y = 0.021x + 0.008$; $r^2 = 0.64$; $p < 0.001$; $F_{1,28} = 53.21$	–	$y = 0.010x + 0.261$; $r^2 = 0.07$; $p = 0.079$; $F_{1,28} = 3.32$	$y = 0.059x - 0.245$; $r^2 = 0.45$; $p < 0.001$; $F_{1,28} = 24.76$
13. Särki	$y = -0.003x + 0.268$; $r^2 = 0.02$; $p = 0.201$; $F_{1,28} = 1.71$	$y = 0.007x + 0.078$; $r^2 = 0.18$; $p < 0.05$; $F_{1,28} = 7.51$	$y = 0.015x - 0.008$; $r^2 = 0.47$; $p < 0.001$; $F_{1,28} = 26.97$	–	–	$y = 0.021x - 0.094$; $r^2 = 0.78$; $p < 0.001$; $F_{1,28} = 106.35$
14. Särkilomp	$y = -0.001x + 0.173$; $r^2 = -0.03$; $p = 0.586$; $F_{1,28} = 0.30$	$y = 0.056x - 0.170$; $r^2 = 0.56$; $p < 0.001$; $F_{1,28} = 37.37$	$y = 0.020x + 0.005$; $r^2 = 0.67$; $p < 0.001$; $F_{1,28} = 58.62$	$y = 0.021x + 0.180$; $r^2 = 0.56$; $p < 0.001$; $F_{1,15} = 21.56$	–	$y = 0.005x + 0.027$; $r^2 = 0.78$; $p < 0.001$; $F_{1,28} = 103.86$
15. Aalis	–	$y = 0.066x - 0.330$; $r^2 = 0.16$; $p < 0.05$; $F_{1,28} = 6.460$	$y = 0.057x - 0.152$; $r^2 = 0.73$; $p < 0.001$; $F_{1,28} = 79.53$	$y = 0.053x - 1.582$; $r^2 = 0.69$; $p < 0.001$; $F_{1,28} = 66.75$	$y = 0.008x + 0.279$; $r^2 = 0.02$; $p = 0.207$; $F_{1,28} = 1.67$	$y = 0.046x + 0.161$; $r^2 = 0.17$; $p < 0.05$; $F_{1,28} = 6.88$
16. Pasma	$y = 0.015x - 0.092$; $r^2 = 0.57$; $p < 0.001$; $F_{1,28} = 39.53$	$y = 0.012x + 0.138$; $r^2 = 0.18$; $p < 0.05$; $F_{1,28} = 7.35$	$y = 0.040x - 0.046$; $r^2 = 0.83$; $p < 0.001$; $F_{1,27} = 141.92$	$y = 0.062x - 1.322$; $r^2 = 0.63$; $p < 0.001$; $F_{1,22} = 40.41$	$y = 0.031x + 0.047$; $r^2 = 0.64$; $p = 0.000$; $F_{1,28} = 51.64$	$y = 0.059x - 0.206$; $r^2 = 0.66$; $p < 0.001$; $F_{1,28} = 56.30$
17. Vaatto	$y = 0.009x + 0.245$; $r^2 = 0.26$; $p < 0.05$; $F_{1,12} = 5.44$	$y = 0.134x - 1.615$; $r^2 = 0.80$; $p < 0.001$; $F_{1,11} = 49.43$	$y = 0.089x - 0.387$; $r^2 = 0.55$; $p < 0.001$; $F_{1,28} = 36.51$	$y = 0.095x - 2.429$; $r^2 = 0.77$; $p < 0.001$; $F_{1,26} = 93.58$	$y = 0.019x + 0.310$; $r^2 = 0.17$; $p < 0.05$; $F_{1,28} = 6.82$	$y = 0.057x - 0.004$; $r^2 = 0.37$; $p < 0.001$; $F_{1,28} = 17.77$
18. Rattos	–	$y = 0.080x - 0.411$; $r^2 = 0.46$; $p < 0.001$; $F_{1,28} = 25.32$	$y = 0.038x + 0.389$; $r^2 = 0.09$; $p = 0.062$; $F_{1,28} = 3.78$	$y = 0.053x - 1.102$; $r^2 = 0.84$; $p < 0.001$; $F_{1,24} = 132.83$	$y = 0.042x + 0.000$; $r^2 = 0.51$; $p = 0.000$; $F_{1,28} = 30.88$	$y = 0.080x - 0.205$; $r^2 = 0.419$; $p < 0.001$; $F_{1,28} = 21.82$

841 *Table S5.* Lake-specific linear regression equations, adjusted R-squared (r^2), p-values and F-values with degrees of freedom between THg
842 concentration ($\mu\text{g g}^{-1}$ dry weight) and fish age for six species. Statistically significant ($p < 0.05$) equations are bolded. Please note that lakes (column
843 No) are ordered by PC1 scores.

844

Lake	Whitefish	Vendace	Perch	Pike	Roach	Ruffe
1. Kilpis	$y = -0.006x + 0.207$; $r^2 = 0.01$; $p = 0.276$; $F_{1,28} = 1.24$	–	–	$y = 0.078x + 0.099$; $r^2 = 0.71$; $p < 0.001$; $F_{1,28} = 74.19$	–	–
2. Tsahkal	$y = -0.016x + 0.571$; $r^2 = 0.05$; $p = 0.115$; $F_{1,28} = 2.65$	–	–	–	–	–
3. Kolta	$y = 0.003x + 0.170$; $r^2 = 0.13$; $p < 0.05$; $F_{1,28} = 5.31$	–	–	$y = 0.060x + 0.263$; $r^2 = 0.87$; $p < 0.001$; $F_{1,14} = 98.48$	–	–
4. Kuohkima	$y = 0.015x + 0.242$; $r^2 = 0.32$; $p < 0.001$; $F_{1,28} = 14.52$	–	–	$y = 0.122x + 0.181$; $r^2 = 0.60$; $p < 0.001$; $F_{1,16} = 26.78$	–	–
5. Oiko	$y = 0.007x + 0.437$; $r^2 = 0.020$; $p = 0.22$; $F_{1,28} = 1.55$	–	–	$y = 0.253x - 0.024$; $r^2 = 0.84$; $p < 0.001$; $F_{1,25} = 133.68$	–	$y = 0.076x + 0.056$; $r^2 = 0.71$; $p < 0.001$; $F_{1,28} = 72.99$
6. Kivi	$y = 0.015x + 0.317$; $r^2 = 0.16$; $p < 0.05$; $F_{1,28} = 6.62$	–	$y = 0.120x - 0.245$; $r^2 = 0.51$; $p < 0.001$; $F_{1,28} = 31.27$	$y = 0.222x - 0.163$; $r^2 = 0.87$; $p < 0.001$; $F_{1,16} = 118.50$	–	$y = 0.071x + 0.064$; $r^2 = 0.66$; $p < 0.001$; $F_{1,28} = 58.20$
7. Ropi	$y = 0.016x + 0.153$; $r^2 = 0.10$; $p = 0.051$; $F_{1,28} = 4.17$	–	–	$y = 0.120x + 0.100$; $r^2 = 0.50$; $p < 0.001$; $F_{1,20} = 22.05$	–	$y = 0.036x + 0.240$; $r^2 = 0.06$; $p = 0.154$; $F_{1,19} = 2.20$
8. Palo	$y = 0.018x + 0.137$; $r^2 = 0.60$; $p < 0.001$; $F_{1,28} = 44.76$	$y = 0.043x + 0.154$; $r^2 = 0.60$; $p = 0.000$; $F_{1,28} = 43.99$	$y = 0.033x + 0.139$; $r^2 = 0.59$; $p < 0.001$; $F_{1,28} = 42.00$	$y = 0.113x + 0.057$; $r^2 = 0.73$; $p < 0.001$; $F_{1,13} = 38.03$	–	$y = 0.027x + 0.155$; $r^2 = 0.37$; $p < 0.001$; $F_{1,28} = 17.86$
9. Vaggoval	$y = 0.040x + 0.181$; $r^2 = 0.36$; $p < 0.001$; $F_{1,28} = 17.17$	–	$y = 0.076x + 0.086$; $r^2 = 0.76$; $p < 0.001$; $F_{1,28} = 90.31$	$y = 0.092x + 0.315$; $r^2 = 0.75$; $p < 0.001$; $F_{1,25} = 79.70$	–	$y = -0.007x + 0.543$; $r^2 = -0.04$; $p = 0.925$; $F_{1,26} = 0.01$
10. Akas	$y = 0.020x + 0.074$; $r^2 = 0.63$; $p < 0.001$; $F_{1,28} = 50.58$	$y = 0.020x + 0.191$; $r^2 = 0.09$; $p = 0.061$; $F_{1,28} = 3.83$	$y = 0.082x - 0.016$; $r^2 = 0.63$; $p < 0.001$; $F_{1,28} = 48.40$	$y = 0.159x + 0.009$; $r^2 = 0.77$; $p < 0.05$; $F_{1,4} = 17.73$	$y = -0.006x + 0.245$; $r^2 = 0.02$; $p = 0.502$; $F_{1,28} = 0.46$	$y = 0.033x + 0.033$; $r^2 = 0.81$; $p < 0.001$; $F_{1,28} = 128.30$
11. Jeris	$y = 0.030x + 0.134$; $r^2 = 0.25$; $p < 0.01$; $F_{1,28} = 10.45$	$y = 0.063x + 0.038$; $r^2 = 0.78$; $p = 0.000$; $F_{1,28} = 104.69$	$y = 0.080x + 0.054$; $r^2 = 0.36$; $p < 0.001$; $F_{1,28} = 15.42$	–	–	$y = 0.032x + 0.113$; $r^2 = 0.61$; $p < 0.001$; $F_{1,28} = 45.44$
12. Toras	$y = -0.001x + 0.235$; $r^2 = -0.04$; $p = 0.918$; $F_{1,28} = 0.01$	$y = 0.043x + 0.180$; $r^2 = 0.59$; $p = 0.000$; $F_{1,28} = 42.30$	$y = 0.050x + 0.150$; $r^2 = 0.39$; $p < 0.001$; $F_{1,28} = 19.78$	–	$y = 0.018x + 0.297$; $r^2 = 0.15$; $p = 0.021$; $F_{1,28} = 5.97$	$y = 0.056x + 0.128$; $r^2 = 0.43$; $p < 0.001$; $F_{1,28} = 22.47$
13. Särki	$y = -0.002x + 0.224$; $r^2 = -0.02$; $p = 0.515$; $F_{1,28} = 0.44$	$y = 0.018x + 0.115$; $r^2 = 0.39$; $p = 0.000$; $F_{1,28} = 19.18$	$y = 0.021x + 0.099$; $r^2 = 0.59$; $p < 0.001$; $F_{1,28} = 42.31$	–	–	$y = 0.022x + 0.064$; $r^2 = 0.88$; $p < 0.001$; $F_{1,28} = 218.05$
14. Särkilom.	$y = 0.000x + 0.154$; $r^2 = -0.04$; $p = 0.937$; $F_{1,28} = 0.01$	$y = 0.109x + 0.054$; $r^2 = 0.44$; $p = 0.000$; $F_{1,28} = 23.56$	$y = 0.048x + 0.085$; $r^2 = 0.67$; $p < 0.001$; $F_{1,28} = 59.76$	$y = 0.122x + 0.549$; $r^2 = 0.49$; $p < 0.001$; $F_{1,15} = 16.28$	–	$y = 0.013x + 0.053$; $r^2 = 0.85$; $p < 0.001$; $F_{1,28} = 161.67$
15. Aalis	–	$y = 0.068x + 0.233$; $r^2 = 0.14$; $p = 0.025$; $F_{1,28} = 5.57$	$y = 0.191x - 0.115$; $r^2 = 0.72$; $p < 0.001$; $F_{1,28} = 77.19$	$y = 0.225x + 0.220$; $r^2 = 0.85$; $p < 0.001$; $F_{1,28} = 169.34$	$y = 0.015x + 0.299$; $r^2 = 0.02$; $p = 0.228$; $F_{1,28} = 1.52$	$y = 0.051x + 0.345$; $r^2 = 0.38$; $p < 0.001$; $F_{1,28} = 18.96$
16. Pasma	$y = 0.058x + 0.077$; $r^2 = 0.77$; $p < 0.00$; $F_{1,28} = 95.79$	$y = 0.020x + 0.280$; $r^2 = 0.06$; $p = 0.111$; $F_{1,28} = 2.72$	$y = 0.108x + 0.099$; $r^2 = 0.74$; $p < 0.001$; $F_{1,27} = 79.19$	$y = 0.315x - 0.527$; $r^2 = 0.63$; $p < 0.001$; $F_{1,22} = 40.63$	$y = 0.036x + 0.214$; $r^2 = 0.66$; $p = 0.000$; $F_{1,28} = 59.00$	$y = 0.069x + 0.032$; $r^2 = 0.68$; $p < 0.001$; $F_{1,28} = 62.08$
17. Vaatto	$y = 0.048x + 0.257$; $r^2 = 0.42$; $p < 0.01$; $F_{1,12} = 10.26$	$y = 0.169x + 0.095$; $r^2 = 0.62$; $p = 0.001$; $F_{1,11} = 20.55$	$y = 0.201x - 0.018$; $r^2 = 0.69$; $p < 0.001$; $F_{1,28} = 66.30$	$y = 0.444x - 0.963$; $r^2 = 0.73$; $p < 0.001$; $F_{1,26} = 73.96$	$y = 0.020x + 0.413$; $r^2 = 0.18$; $p = 0.011$; $F_{1,28} = 7.52$	$y = 0.038x + 0.275$; $r^2 = 0.48$; $p < 0.001$; $F_{1,28} = 27.75$
18. Rattos		$y = 0.123x + 0.177$; $r^2 = 0.68$; $p = 0.000$; $F_{1,28} = 62.94$	$y = 0.145x + 0.254$; $r^2 = 0.25$; $p < 0.01$; $F_{1,28} = 10.76$	$y = 0.257x - 0.040$; $r^2 = 0.79$; $p < 0.001$; $F_{1,24} = 92.09$	$y = 0.042x + 0.272$; $r^2 = 0.50$; $p = 0.000$; $F_{1,28} = 29.73$	$y = 0.077x + 0.086$; $r^2 = 0.72$; $p < 0.001$; $F_{1,28} = 75.07$

846 FIGURE CAPTIONS

847 **Fig. S1.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
848 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in whitefish.
849 Numbers in each figure refer to the study-lake order based on PC1 axis scores (see the
850 corresponding lake names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

851

852 **Fig. S2.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
853 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in vendace.
854 Numbers in each figure refer to study-lake order according to PC1 axis scores (see the corresponding
855 lake names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

856

857 **Fig. S3.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
858 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in perch.
859 Numbers in each figure refer to study-lake order according to PC1 axis scores (see the corresponding
860 lake names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

861

862 **Fig. S4.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
863 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in pike. Numbers
864 in each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake
865 names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

866

867 **Fig. S5.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
868 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in roach.

869 Numbers in each figure refer to study-lake order according to PC1 axis scores (see the corresponding
870 lake names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

871

872 **Fig. S6.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
873 (hatched line) between total length (cm) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in ruffe. Numbers
874 in each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake
875 names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

876

877 **Fig. S7.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
878 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in whitefish. Numbers
879 in each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake
880 names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

881

882 **Fig. S8.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
883 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in vendace. Numbers
884 in each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake
885 names in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

886

887 **Fig. S9.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
888 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in perch. Numbers in
889 each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake names
890 in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

891

892 **Fig. S10.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
893 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in pike. Numbers in
894 each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake names
895 in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

896

897 **Fig. S11.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
898 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in roach. Numbers in
899 each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake names
900 in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

901

902 **Fig. S12.** Bioaccumulation of THg using linear regression (solid line) and 95% confidence intervals
903 (hatched line) between age (years) and THg concentration ($\mu\text{g g}^{-1}$ dry weight) in ruffe. Numbers in
904 each figure refer to study-lake order according to PC1 axis scores (see the corresponding lake names
905 in e.g. Table 1). Only significant ($p < 0.05$) regression lines are presented.

906

907 **Fig. S13.** Assessment of putative relationships between PC2 (indicating lake morphometry; please
908 note that opposite lake score values are used for clarity) and total length- (cm, uppermost row) and
909 age-adjusted (second row) THg concentrations ($\mu\text{g g}^{-1}$ dry weight), as well as THg bioaccumulation
910 rate relative to total length (cm, third row) and age (lower row). Roach was excluded from the
911 analyses of THg bioaccumulation rate (Slope) due to low sample size. For equations see Table 3. No
912 significant regressions were detected for any of the six species.

913

914 **Fig. S14.** Linear relationships between PC3 scores (indicating catchment magnitude; please note that
915 opposite lake score values are used for clarity) and length- (cm, upper row) and age-adjusted

916 (second row) THg ($\mu\text{g g}^{-1}$ dry weight), as well as THg bioaccumulation rate (slope of lake and species-
917 specific linear regression) relative to total length (third row) and age (lower row). Only significant
918 regression (solid line) and 95% confidence limits (hatched line) are presented. Roach was excluded
919 from the analyses of THg accumulation rate (Slope) due to low sample size. For equations see Table
920 3.

921

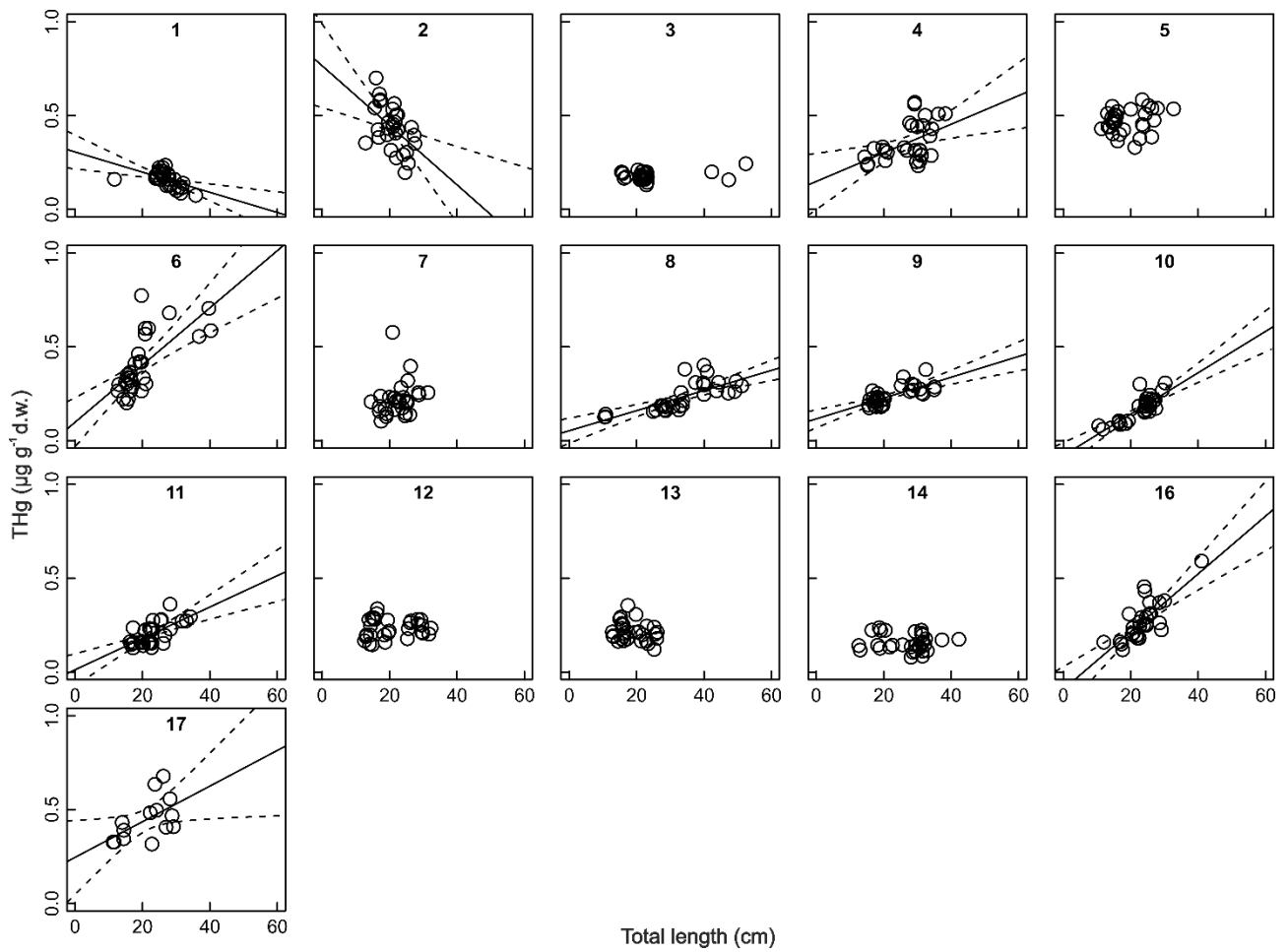


Fig. S1. Whitefish

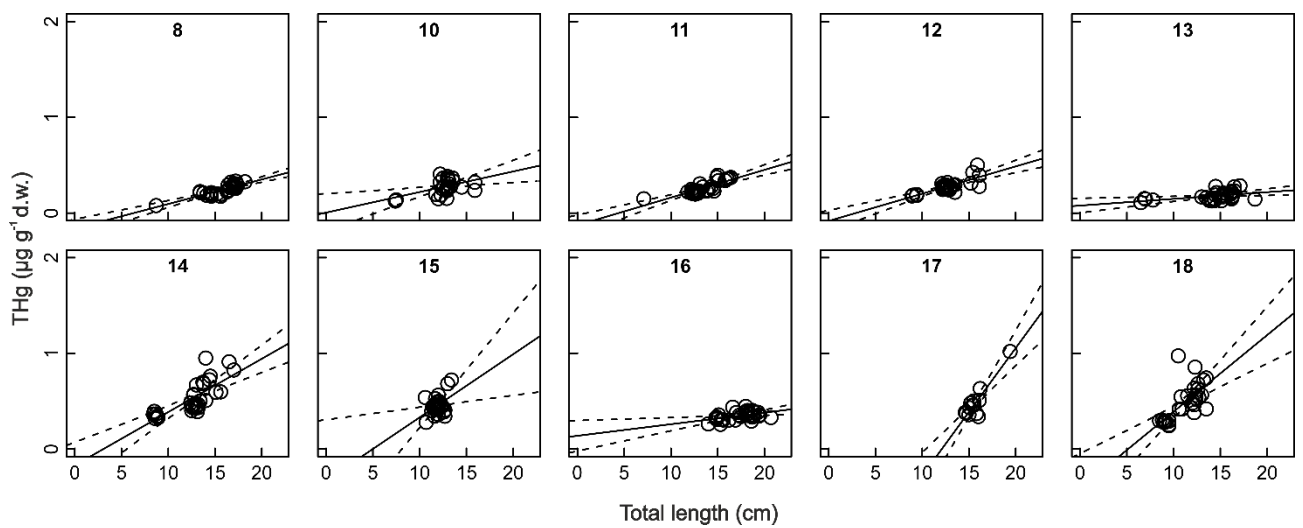


Fig. S2. Vendace

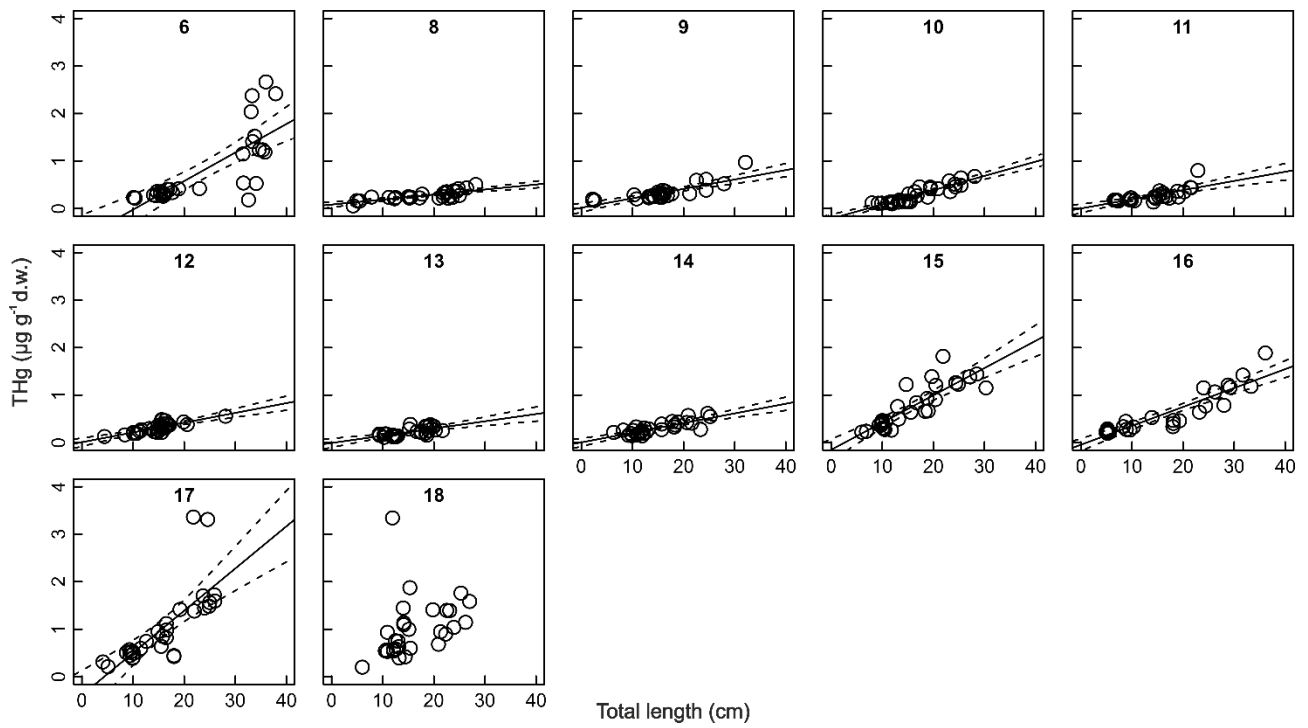


Fig. S3. Perch

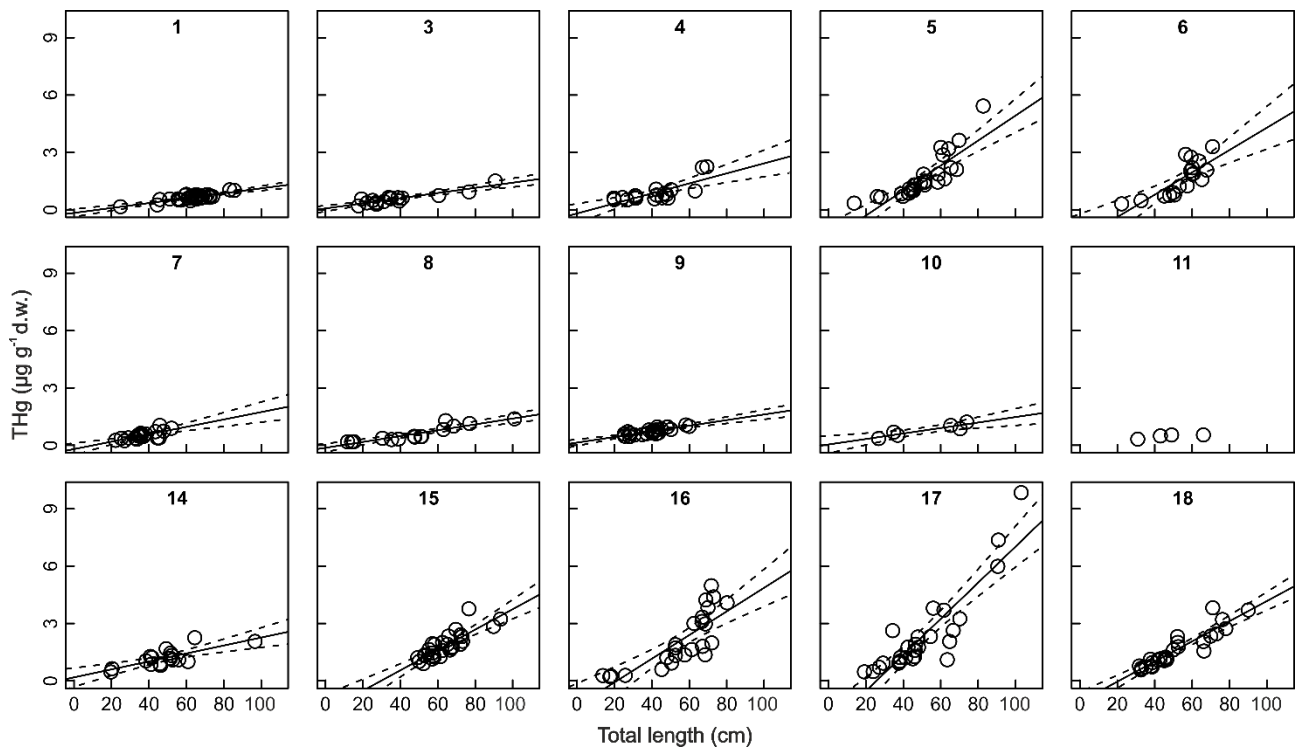


Fig. S4. Pike

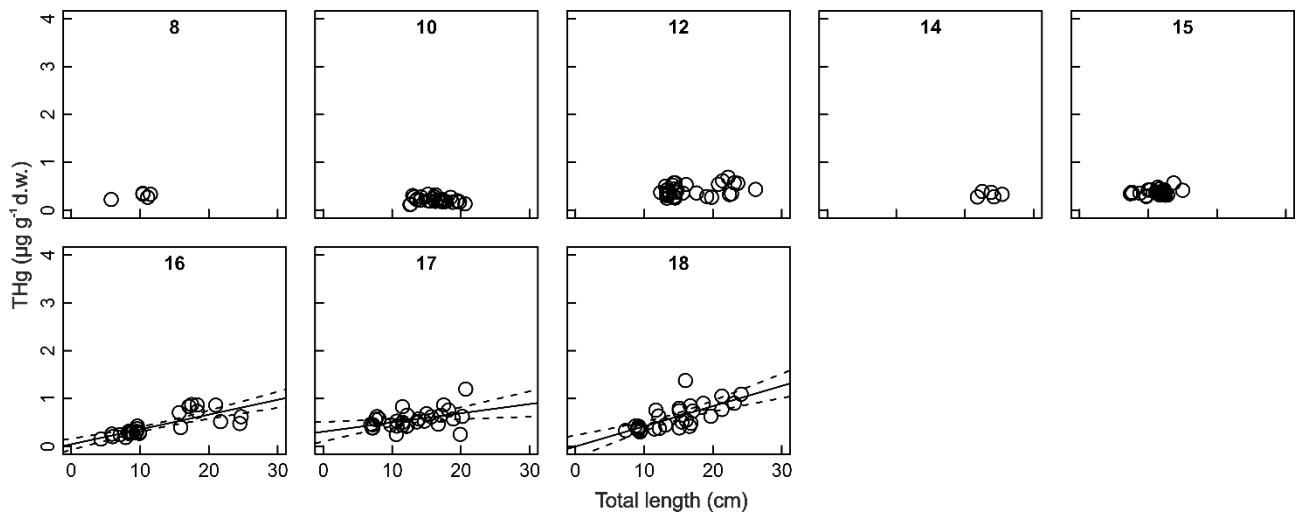


Fig. S5. Roach

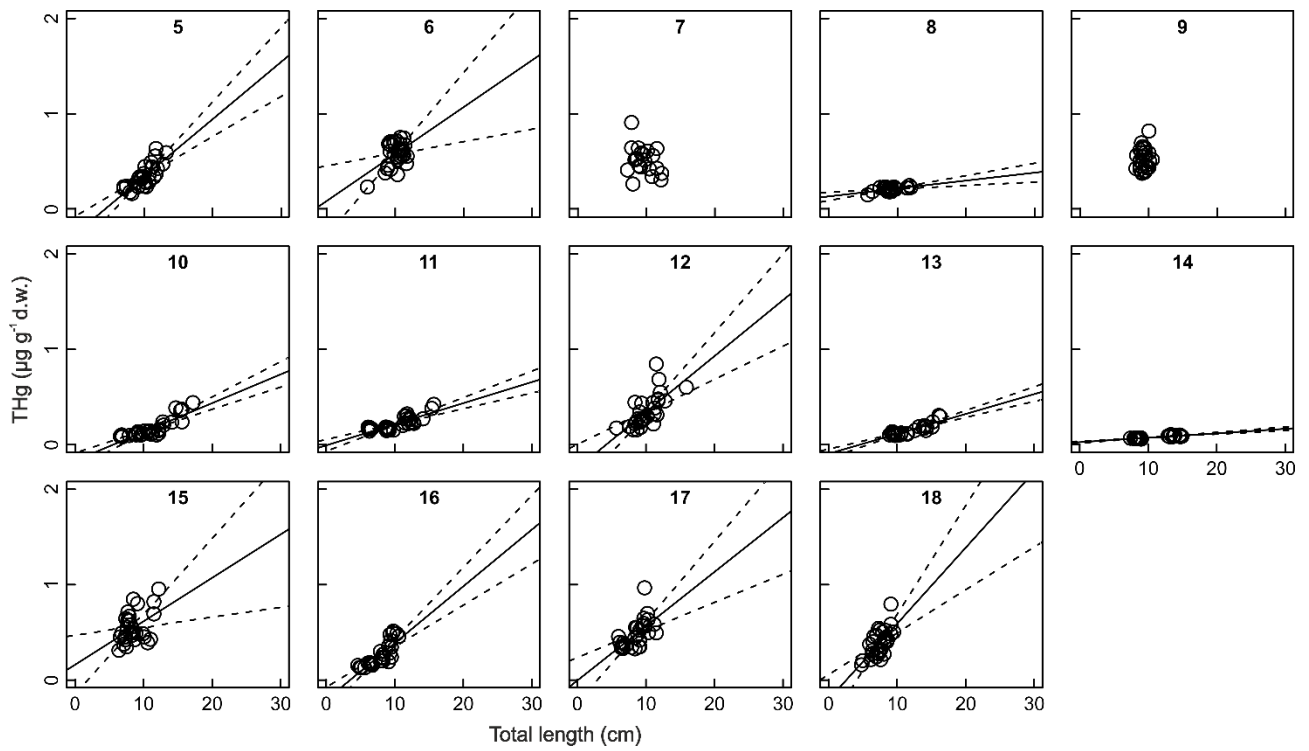


Fig. S6. Ruffe

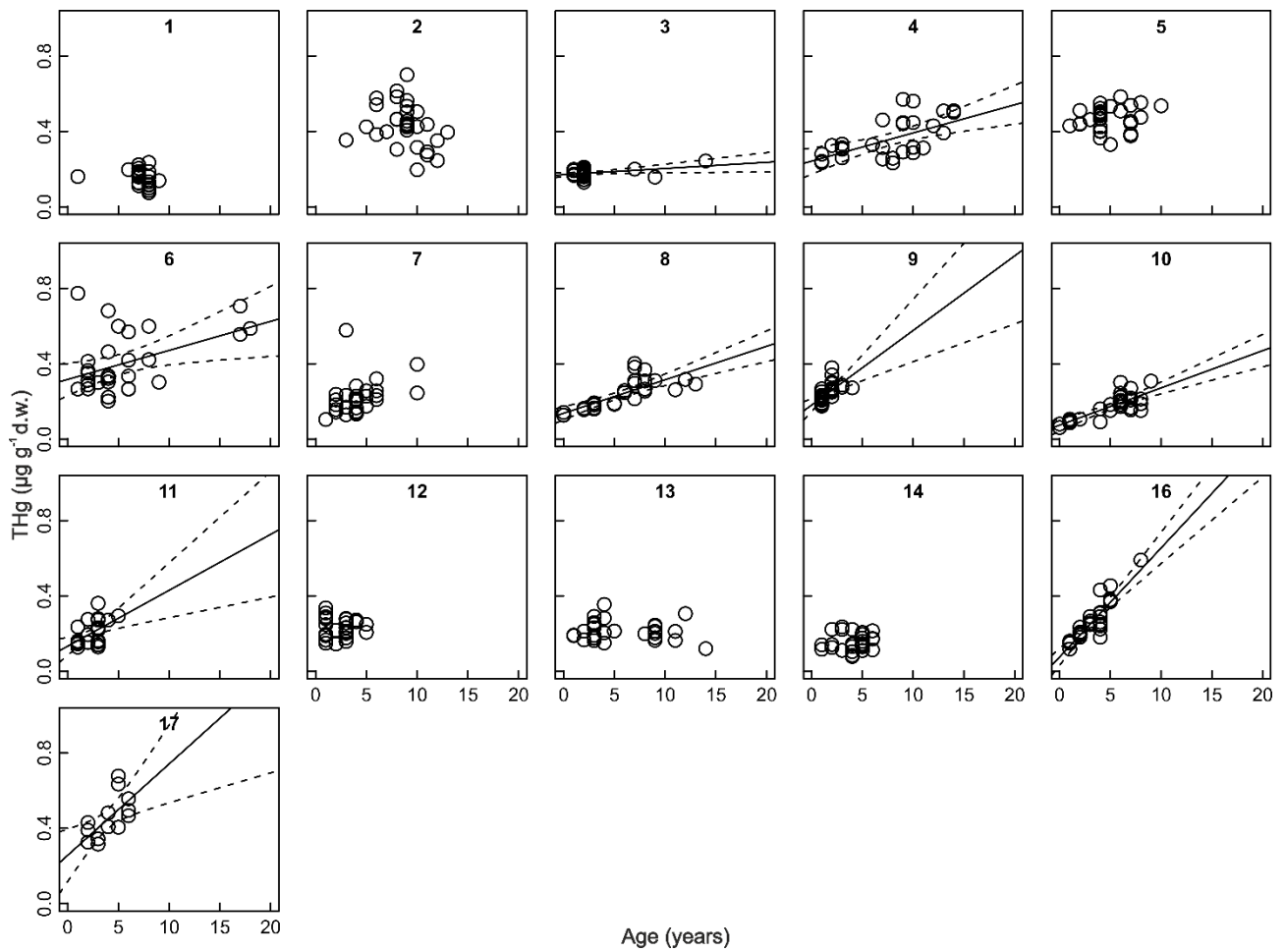


Fig. S7. Whitefish

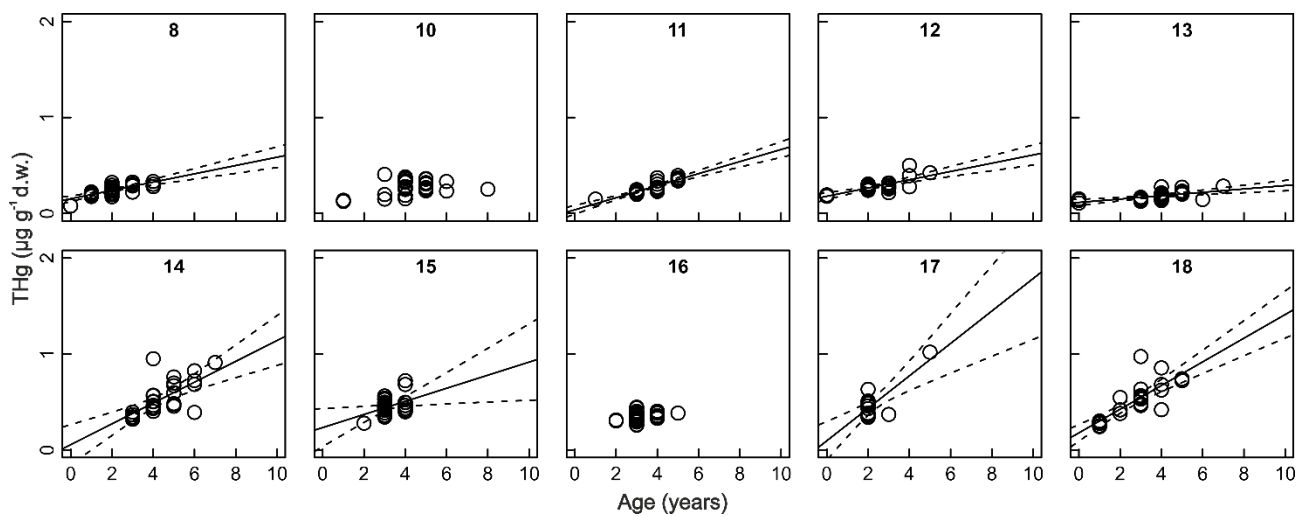


Fig. S8. Vendace

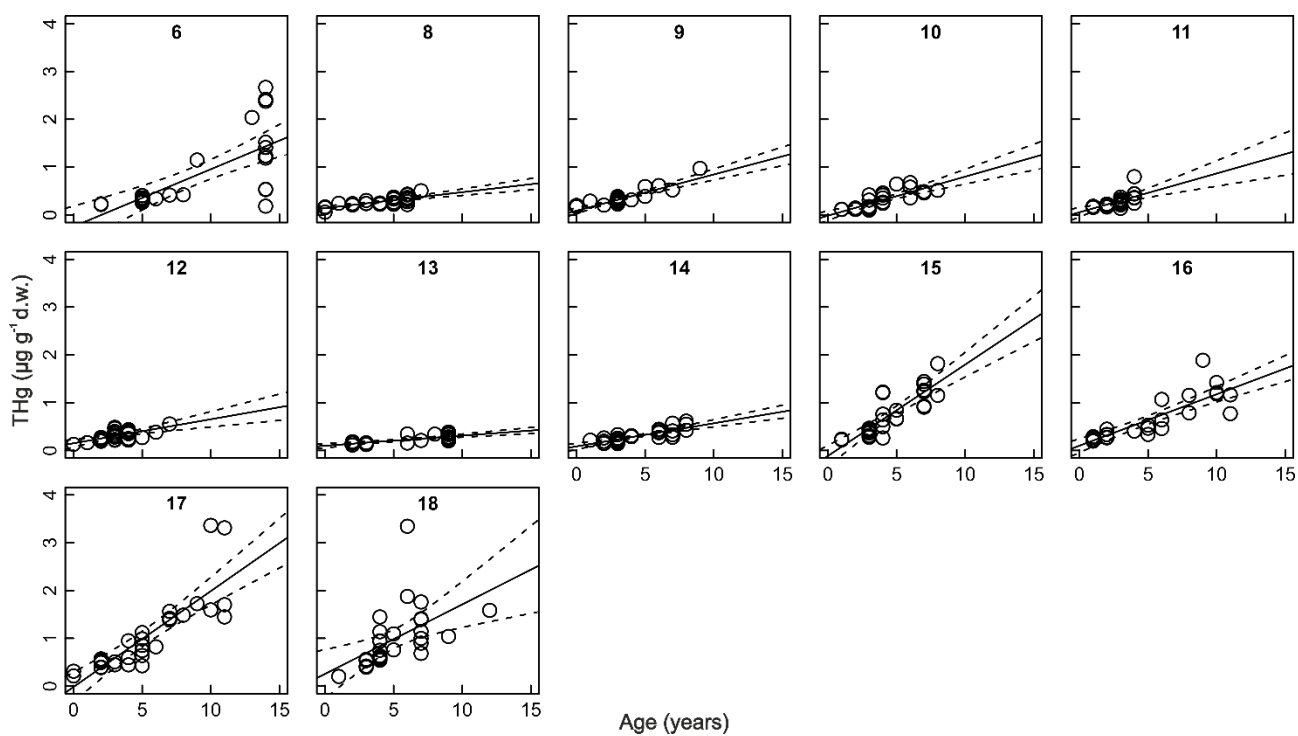


Fig. S9. Perch

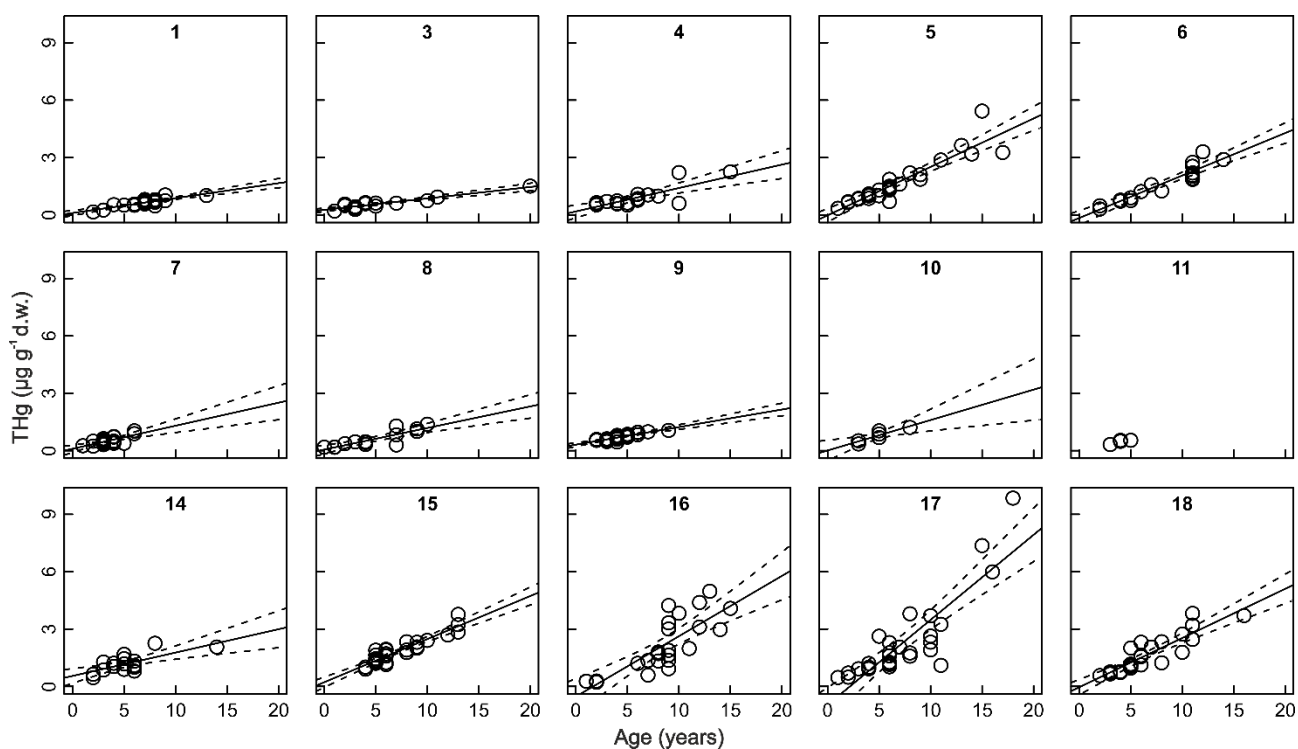


Fig. S10. Pike

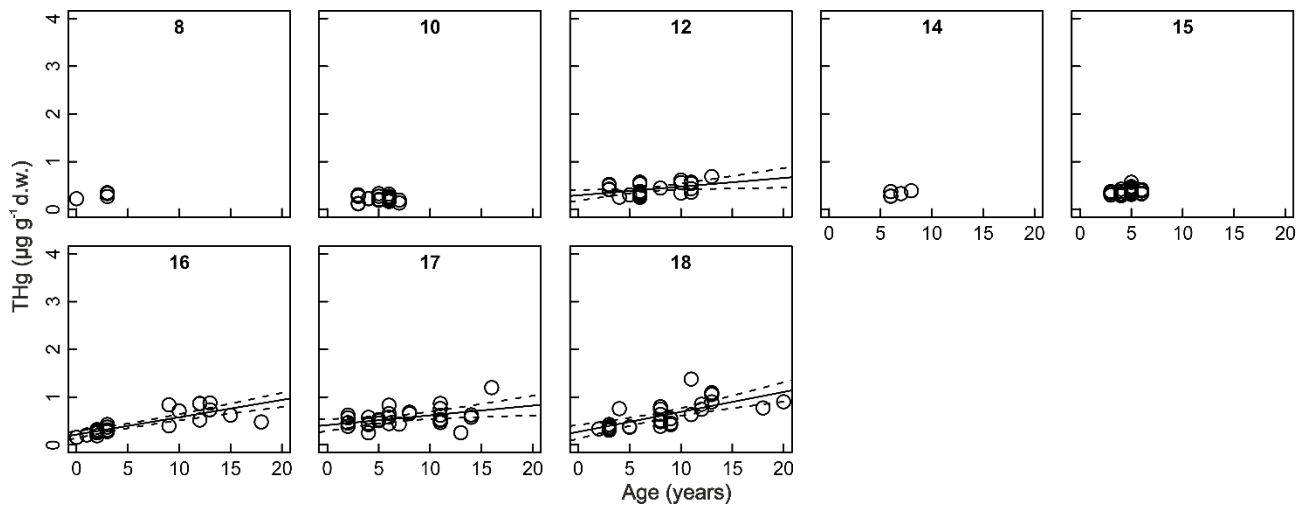


Fig. S11. Roach

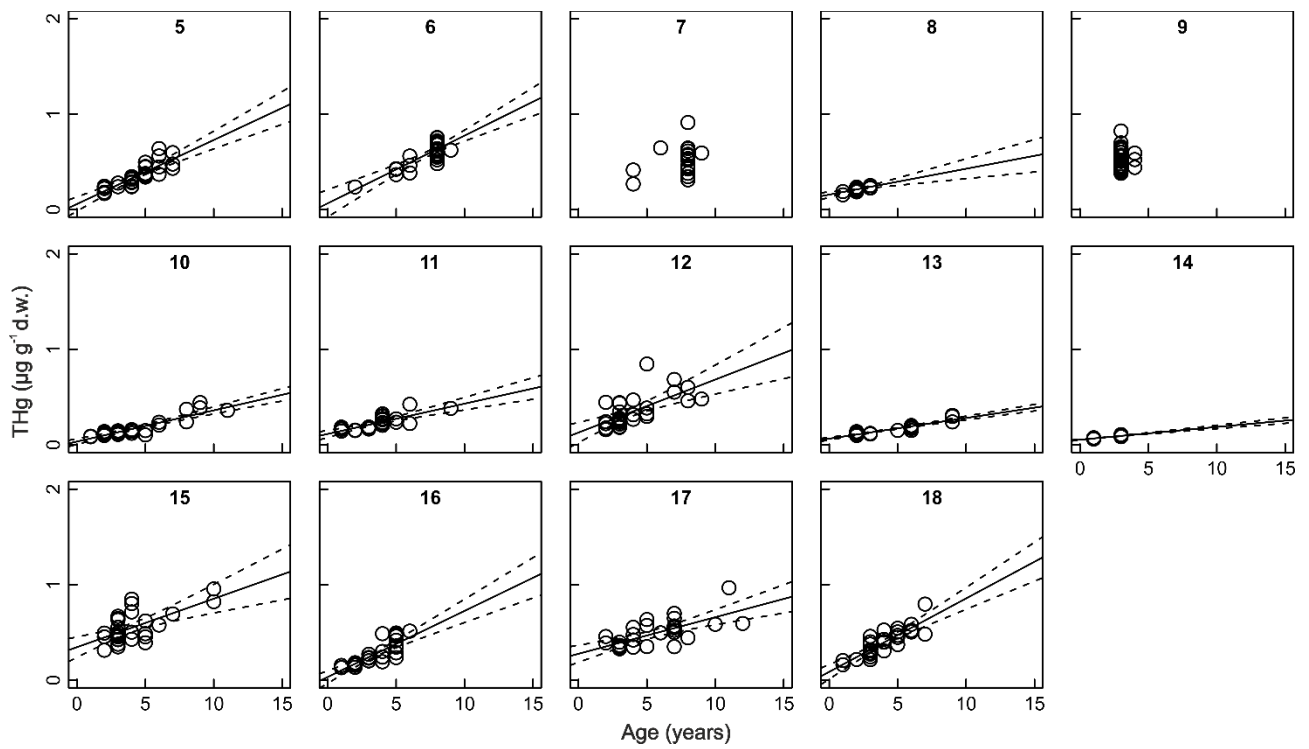
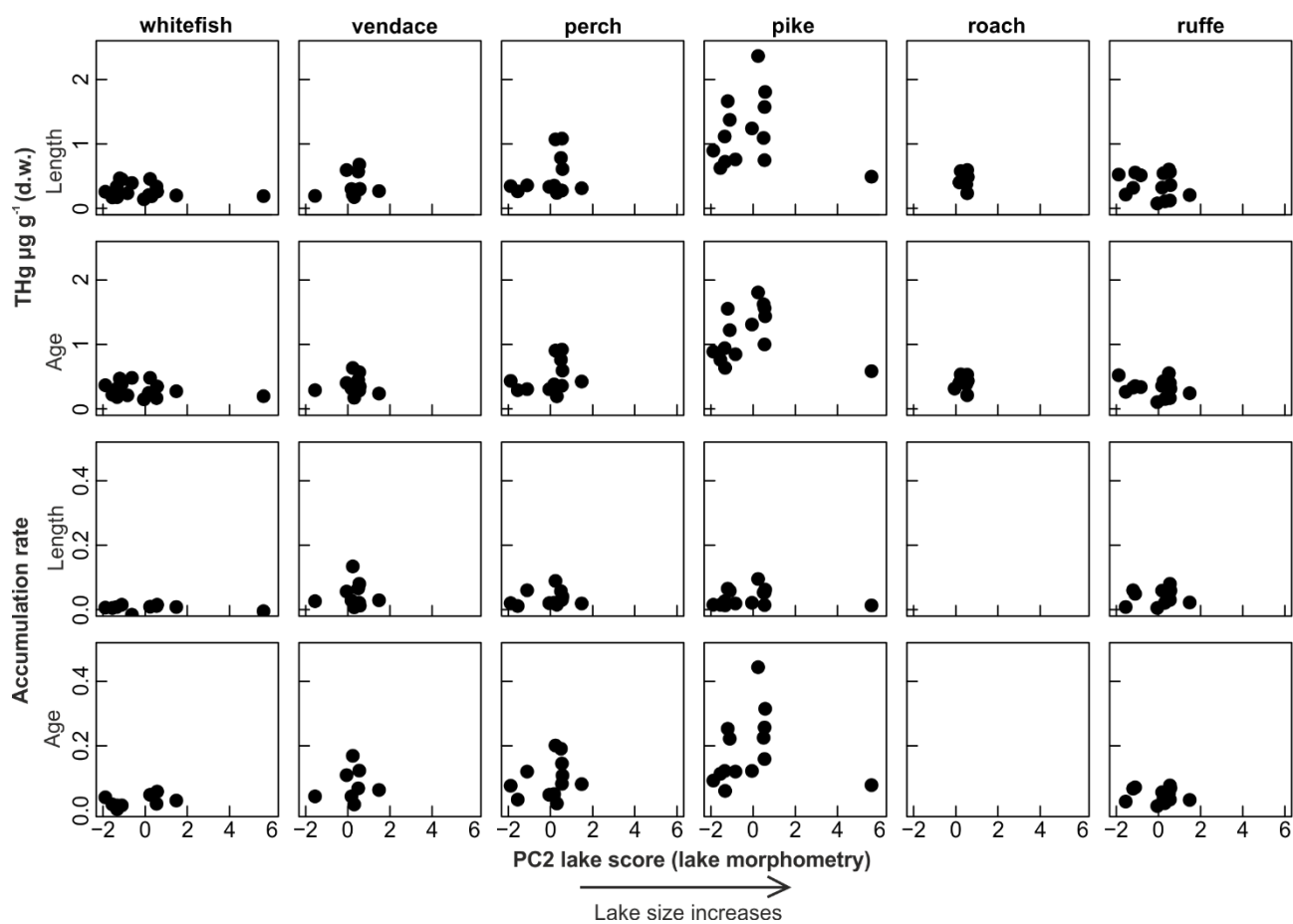
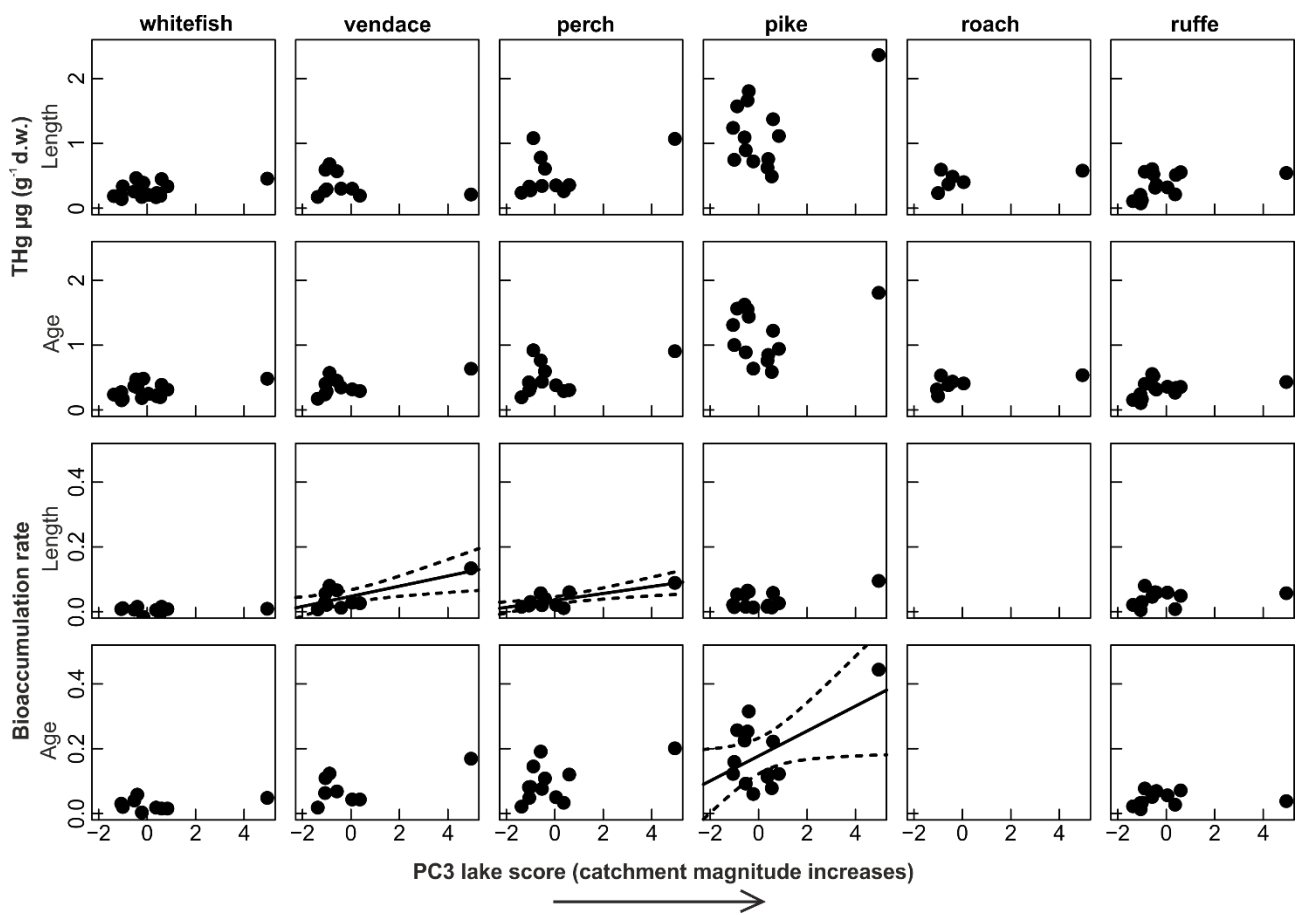


Fig. S12. Ruffe



961

962 Fig. S13.



963

964 Fig. S14